ANTS

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ILLUSTRATIONS

CHAPTER I

INTRODUCTORY

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INTRODUCTORY

THE social insects in general, and ants in particular, are, with birds and with man, the fine flowers of the tree of life. Had not their advance to greater size and strength been checked through limitations inherent from the first in the fundamentals of insect organization, they might well have evolved into beings so formidable as to have held the vertebrates back in their conquest of the land, and for ever prevented the development of man.

Innumerable comparisons have been made between human society and the social organization of ant, bee, or termite; theories have been advanced and morals pointed, Utopian schemes encouraged and whole theories of the State built up for man on the basis of analogy with these little insects. Almost without exception the moral has been false, the analogy misleadingly used. It will be well to point out at the start some of the radical differences between social insects and social man.

In the first place, the development from nonhuman to human mammal has occurred but once,* while the transition from non-social to social insects has occurred on a number of separate occasions. Three main grades of social habit may be distinguished. In the lowest there is some sort of a family life, either the mother or both parents living with and helping the developing young. This may be called the subsocial, or family, grade. The second is the true social, or colonial, grade, in which the young, when fully grown, stay with their parents and coöperate with them in building the nest and caring for further broods of young. The highest grade is that of the caste-society, in which some of the young are transformed into unsexed "neuters," who take off the shoulders of the fertile caste all the duties of the colony, save only that of reproduction.

According to W. M. Wheeler, the great authority on the biology of these animals, some grade

* There are still one or two authors who uphold the polyphyletic, or multiple, origin of man. It is, however, extremely improbable that they are right; and even if they were, they only suppose that the different races of man have evolved from different types within the one small group of anthropoid apes. The multiple origin of social insects is an origin from a number of quite separate and radically different orders or sub-orders, as different as rodent from carnivore, as elephant from ruminant.

of social life has been reached no less than twenty-four times in the evolution of insects, among the representatives of five separate orders. If we deduct the merely subsocial types, ten separate attainments of the true social level remain, distributed between the orders of Hymenoptera and Isoptera. Among the Hymenoptera, Wheeler believes that full social life has been acquired five separate times by wasps, three times by bees, and once by ants. Even if we suppose that ants—all members of which are social—arose as an offshoot of an already socialized wasplike form, it is at least certain that bees and wasps have developed their extremely similar societies quite independently of each other; and, in addition, the caste-system has been evolved at least two or three separate times in wasps, and at least twice among bees; finally, the Termites have developed social life and a caste-system quite separately from the Hymenoptera, and along rather different lines.

An even more striking difference between social insects and man concerns the number of species which exist in the two types. There is but one human species now extant. Even if we take all known fossil forms into account, we can only muster half a dozen at the most. Of fully social insects, on the other hand, there have been described about 800 species among wasps, about 500 among bees, over 3,500 among ants, and over 1,000 among termites—nearly 6,000 in all; and when we reflect that systematists are discovering scores of new species, notably from the tropics, every year, we shall probably not be making an over-estimate if we say that 10,000 separate species of social insects are in existence.

The reason for this is partly, though not mainly, to be sought in another biological difference between man and the social insects. Man dates back only to the Pliocene or perhaps Miocene;* and *Homo sapiens* appears to have arisen only during the Pleistocene, less than one million years ago. Social ants, bees, wasps, and termites have all been found in Baltic amber, which exuded from pines growing in what to-day we call Sweden, right back in Lower Oligocene times, about thirty million years ago. In Wheeler's own words, "My study [of these ants trapped in that long-ago resin] showed conclusively that the ants have undergone no important structural modifi-

*The geological periods mentioned are arranged in the following order, from the present back: Pleistocene, Pliocene, Miocene, Oligocene, Eocene, Cretaceous, Jurassic, Triassic.

Photo by Martin Duncan

Ants are no longer evolving. A winged ant, similar in all essentials to ants of to-day, preserved in Baltic Amber, and therefore dating back about 30 million years (p. 61).

cations since the Lower Oligocene, that they had at that time developed all their various castes . . . that they attended plant-lice, kept guest beetles in their nests, and had parasitic mites attached to their legs in the very same peculiar position as in our living species." Many modern genera were already in existence, and some of the Oligocene species were practically indistinguishable from those of to-day. Typical ants have been found in the Eocene, and the strong probability is that several branches of the Hymenoptera became fully social at least as early as the Cretaceous.

Even if we take Upper Cretaceous and Lower Pliocene as the two dates in question, social insects have been in existence well over five times as long as even the most primitive man; and the ratio, if we take the Triassic for the ants, and the Old Stone Age for man, becomes more like a hundred times.

This difference in evolutionary past has another aspect. We have just seen that the societies of ants have changed extremely little since the Oligocene, about thirty million years ago. But we all know that the societies of man have changed profoundly since man's origin, and, what is more, that the change shows no sign of abating into a stable phase, but has, rather, been progressively accelerated throughout man's history. This points the way to the last and most fundamental distinction of all, on which all the others hinge—the difference in the very structure of the societies and in the whole type of behaviour of the two kinds of organism. The ant imago, or adult, appears upon the scene full-grown, with a full complement of diverse instincts, and does not require any teaching to be able to carry out all the duties biologically required of her. True that she possesses a quite definite, if restricted, power of learning, but this enables her only to adapt her instinctive behaviour to this or that detailed difference of the environment, not to ascend to wholly new levels of behaviour. Furthermore, the major part of the division of labour in an insect society is predetermined by the structure of body and brain. Usually the different castes are of different structural pattern. The smallest neuters of many legionary ants are several hundred times less bulky than the males or females (as well as being of quite different appearance), those of Carebara well over a thousand times; the head of the soldier of the harvesting ant Pheidole is bigger than all the rest of the animal put together, while in the worker it is of normal proportions. The worker bee not only has a larger brain than the queen, but has her legs equipped by heredity with all the tools and gadgets needful for collecting and carrying pollen. Occasionally a division of labour is secured by means of a succession of different instincts in time. The young worker honey-bee helps tend the brood, but there comes a time when she abandons this and begins collecting nectar and pollen. This change of habit has nothing to do with learning, but depends on some development within the brain, as definitely as does the change from tadpole into frog depend on material changes in the body.

On the other hand by far the greater part of division of labour in human society is not predetermined through inborn structure, but is the result of learning. Even where a caste-system has been in operation for centuries, it has had negligible effects upon man's all-round capabilities. Man does not find his tools growing upon his body; he has to make them in infinite variety. His instincts are less specific than the insects', and are gradually overlaid by habit, experience and intelligent purpose until all trace of the original purely instinctive actions are supplanted by learnt behaviour, often of wholly new type, the instinct being merely the buried conduit along which the impulse to action must flow for part of its course. And finally man alone among animals has come to possess conceptual thought and a cumulative tradition. It is this cumulative tradition, based upon rapid learning and conceptual thinking, which has allowed human society to make such rapid evolutionary progress. What is more, the plasticity thus gained has made it possible for man to exploit all the regions of the globe, from Greenland to the tropical jungles, from the Sahara to the Alps, and to reap the advantages of the most varied modes of life, from miner to office clerk, fisherman to factory worker, while still remaining contained within the limits of a single biological species. The social insects achieve the same result, of exploiting the most diverse geographical regions and ways of life, but they can only do so by quite other means. Since their achievement is based almost wholly on ready-made structure, whether the obvious structure of bodily tools, or the concealed but none the less real nerve-structure which is the physical basis of instinct, they can only adapt themselves to large changes of surroundings or way of life by means of alterations in their inherited construction. In other words, they must rely for their adaptations on mutations in their hereditary constitution, which is, of course, in the absence of further mutations, fixed and stable. Thus, while in man each new mode of life requires only a new habit and tradition flowering out of the old germ-plasm, in the insect it demands a new species with changed germ-plasm. The social insects thus exploit the world as a group of separate species, uncombinable biological units, man as a single biological unit, the separateness of whose minor groups is in the main transitory and preventable.

This difference is a particular case of a general principle of evolution. Wherever there exists specialized detailed adaptation, whether of bodily structure or behaviour, there we find groups with a great multiplicity of separate species; wherever structure or behaviour is either generalized or plastic, there we find fewer species in the group. This principle works both when specialized are contrasted with primitive groups, and when they are contrasted with progressive but plastic forms.

To take the contrast of specialized with primitive, there are many more species of bony than of gristly fish, of Pliocene mammals than of Eocene mammals, of insects than of Annelid worms. If we contrast less plastic with more plastic, there are many more birds than mammals, and this again in spite of the birds' greater mobility; more snails than cuttlefish and octopuses, more monkeys than apes. Finally, man, on account of his almost unlimited plasticity, takes living matter on to a new level, where the most extensive adaptation can be achieved, and the whole group yet remain constituted by a single species. Man and the insects thus make the most complete contrast in this respect—the two most successful biological groups in existence, one consisting of nearly half a million kinds, the other but of one. And this consequence is in the long run a cause of the limitation of progress in the less plastic, of further progress in the more plastic.

There is every reason for believing that ants have long since reached the highest level possible to them, and equally every reason for believing that man is only at the bottom of his evolutionary ladder.

CHAPTER II

THE ANT STATE

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THE ants are of all the social insects the most successful and perhaps the most extraordinary. All their more than 3,000 species are social, and show caste-differences, although their societies vary enormously both in size and complexity. Some species boast no more than a few dozen individuals to a nest, whereas in forms like Atta a single colony may muster half a million.

Ants (save a few monstrous queens, sluggish and bloated with eggs) never attain the individual size of some wasps and bees. Even the largest neuter ants fall far short of a gram in weight; in other words, it would take well over a hundred thousand of them to outweigh an average man. The range of adult ant-size, however, is much greater than that of man. Even if we include dwarfs at one end and monstrosities of fat at the other, the largest human being weighs not more than twenty-five or thirty times as much as the smallest; while if we include normal specimens the figure will be reduced to under ten times. But the tiniest ants, like the smallest workers of Carebara, weigh several thousand times less than their largest relatives. Even in one and the same colony, individual bulk may vary up to a thousand times, as in Carebara again, or nearly to the same extent as if Lilliput were sober truth, and Lilliputians and normal men and women lived side by side in one community.

The dwellings of ants are usually underground, and are always characterized by great irregularity of construction as compared with those of bees or wasps. Gone are the honey cells, gone the separate room for each grub. What remains is an irregular series of chambers, connected with each other and the exterior by an equally irregular series of passages. Owing to this lack of geometrical precision, their constructions are less immediately interesting to us; none the less, their irregularity is really a sign of evolutionary advance, for it means that their habits are much more plastic and adaptable, and that, if conditions become unfavourable, the old nest can be abandoned and a new one constructed with a minimum of time and labour. The same is true of their care of their young. The young have no fixed and permanent cribs, but are carried from chamber to chamber as convenience and the conditions of moisture and temperature dictate; the pupæ may even be taken out for a sun-bath, and the whole brood may be rushed to a place of safety when the nest is disturbed.

This method obviously has direct advantages over the more mechanized procedure of the bees. It also has indirect advantages, in that it assures the workers a much more permanent and intimate contact with their young; and this cannot fail to have reacted upon the evolution of their minds.

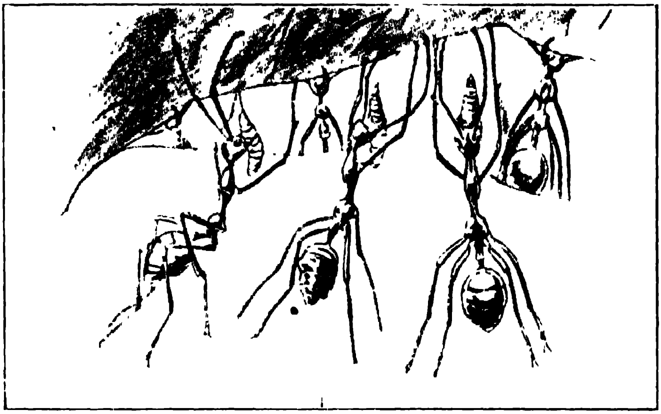
If this continued contact with their helpless charges has favoured the growth of many social qualities of their nurses, the intimate contact with their surroundings fixed upon them by their terrestrial habits must have favoured intelligence and pertinacity. As Espinas pointed out half a century ago, in regard to this very point, "on the earth there is not a contact that does not yield precise information." We may add that the obstacles to be constantly overcome (think what a formidable jungle is the grass to an ant dragging its prey, what an Amazon is every streamlet!) must provoke the development of perseverance and ingenuity. Further, "to employ matter is easier for a terrestrial than an aerial animal. The latter, when it is necessary to build, must, like the bee, either secrete the substance of its nest, or seek it at a distance, as does the bee when she collects propolis, or the wasp when she gathers material for her paper. The terrestrial animal has its building materials close at hand, and its architecture may be as varied as these materials." Ants, therefore, probably owe their "social and industrial superiority to their habitat."

It may be added that their dietary habits are equally plastic and varied, as we shall see in a later chapter. The bees confine themselves to nectar and pollen; the wasps live mainly upon other insects, with nectar and very rarely pollen as subsidiary foods; the termites are wholly vegetarians and mainly cellulose-eaters; but the ants eat not only insects and other animals alive or dead, but seeds, fungi, nectar, the honey-dew voided by plant-lice, and many substances which they find in the storehouses and kitchen cupboards of man. Some single ant species have been broken through the all-but-universal rule of food specialization among the insects and have become prodigies in their group by being practically omnivorous.

Most ant-nests, as we have said, are usually irregular and subterranean; but in most cases the excavated earth is thrown out above ground in the form of mounds, and these may be large and be tunnelled and chambered like the rest. Sometimes the main nest is above ground, like the familiar mounds of the big wood-ant of Europe, built of twigs and pine-needles, to three or four feet high. In the tropics and sub-tropics, however, a much greater range of constructional method obtains. Some ants make earth-nests high above ground by plastering earth round the branches of trees; others have reverted to the use of carton like the wasps, and suspend their tough papery dwellings from boughs; others inhabit natural cavities in trees or shrubs; and still others build nests of leaves.

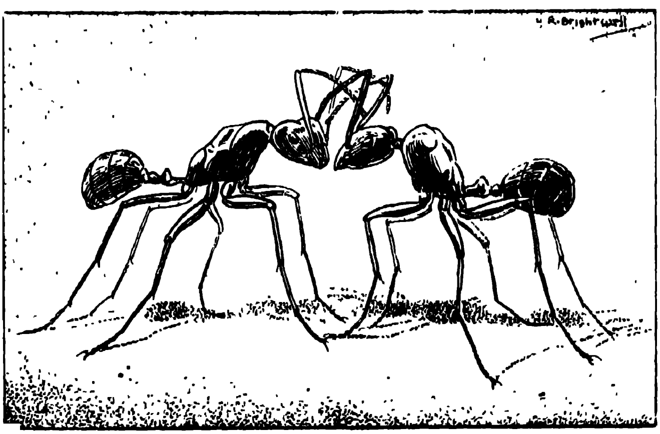
Some of the cavity-dwellers live, not in accidental cracks or rotten holes, but in tubes or chambers which exist as part of the normal structure of certain plants. The fact has given rise to long controversy, some maintaining that the existence of these cavities is quite accidental, while others assert that this is a case of mutual advantage, the presence of the ants helping to protect the plant, and the cavities having thus been developed by natural selection to attract and retain the ants. The second supposition is rendered *a priori* probable by the constancy with which certain ants inhabit only certain cavity producing trees, and also by the elaborateness of some of the cavities. But it cannot be said that proof has yet been obtained of the advantages supposed to accrue to the plant, so that the matter is still in suspense.

Some of the leaf-builders provide us with a very startling piece of behaviour: they employ child labour. Doflein records how he deliberately made a small hole in such a nest. Almost immediately a number of workers ran up on the outside and, beginning where the rent was narrow, pulled its two edges together, holding on to one side with their jaws, to the other with their feet, and so gradually approximating the edges throughout its length. Meanwhile another gang of workers had swarmed up on the inside. These were carrying larvæ in their jaws. When the outside gang had pulled the edges into position, those on the inside began squeezing their charges with their jaws. On this the larvæ started to secrete abundantly from their salivary glands. The secretion is strongly adhesive, and the workers use it to stick the edges of the tear together, passing the larvæ to and fro from one edge to the other like so many



From "The Science of Life" by H. G. Wells, J. S. Huxley and G. P. Wells. (Waverley Book Co., Ltd.)

(*a*) Child Labour among Ants. Œcophylla workers using their grubs to repair a rent in their nest (p. 20).



(*b*) Ant "Language." Two worker ants (Formica) establishing communication by means of smell and touch with their antennæ (p. 49).

living shuttles. This same method is also used in the normal building of the nest. The differences between human and ant behaviour are beautifully illustrated by these ants. In so far as the ants adapt their weaving movements to the form of the rent, they are exercising a low but definite form of intelligence. But the basis of the whole action, the utilization of the larvæ, is instinctive. The actual structure of the larvæ is hereditarily altered in relation to their use as builders' tools. Not only are their salivary glands much larger than normal, but their saliva is unique in its stickiness. Without these genetic alterations, which the ants are no more able to bring about than we have consciously brought about the presence of hydrochloric acid in our stomachs or the shape of our bones, the actions of the workers would be entirely useless in the building of the nest.

CHAPTER III

LIFE HISTORY

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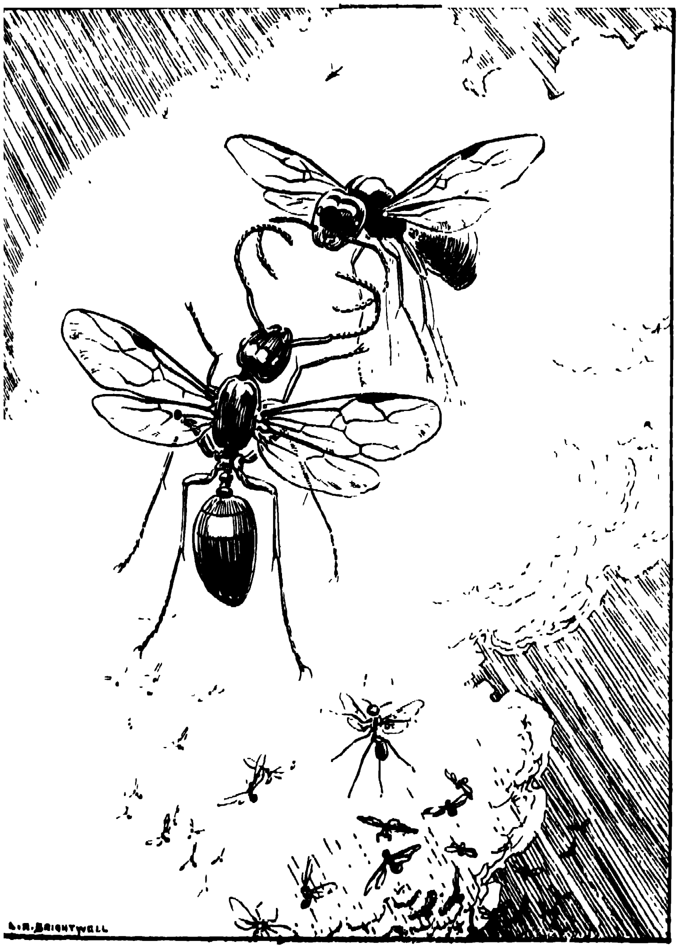
In all but the few parasitic ants, which will be described later, the method of founding new colonies is essentially similar throughout the group.

Only the males and females are winged, and they leave the nest for the nuptial flight, usually in swarms of many males and many females from each nest. Any country dweller knows how sometimes the air will be filled for miles with the flying sexual forms of some common kind of ant. Usually these mass exoduses from the subterranean nest-chambers to the free air occur on still, sultry days; and there seems no doubt that particular weather conditions stimulate the males and queens to fly out, thus insuring that many nests shall discharge their reproductive units at the same time, and so promote cross-fertilization between nests.

Neither the short-lived males nor the long-lived queens use their wings save on this one occasion. Fertilization takes place in the air, and the queen, the hundreds of thousands of spermatozoa needed for the rest of her career now safely stored in the little bag, with the tight purse-strings of muscle round its neck, which opens out of her genital tract, descends to earth. There she casts her wings and either digs a little chamber in the soil or finds one ready made under stone or bark. This done, she closes the door of the cell and becomes a voluntary prisoner. Strange to say, the eggs in her ovaries are unripe and minute at the moment of her flight—perhaps in order to save weight and make flight easier—and must now take weeks or even months to ripen. What is more, these weeks or months must be spent without food.

It is the same problem which confronts the migrating salmon, who does not feed in fresh water on his journey to the spawning-grounds; and it is solved in a somewhat similar but neater way. Large muscles are, of course, required for flying. The shedding of the wings influences these muscles in some specific but not understood way, so that they break down and their substance dissolves and is gradually passed into the blood. This, and the stored fat in her abdomen, constitute the queen's internal food-store. Nourished by this,

Plate III



THE NUPTIAL FLIGHT (p. 25). A male (below) and a female of the red ant, *Myrmica rubra*, about to mate.

she matures and lays her eggs, and then, when they hatch, feeds the grubs with her saliva. This food is, of course, not very abundant, and as a result the first workers to emerge are always abnormally small. They at once dig their way out, find food, and take charge of the second batch of young.

The rearing of the young is no light task. In the first place, the eggs appear incapable of hatching unless continually licked by the workers; they must also be carried from place to place according to the conditions of temperature and moisture within the nest. Similar treatment is accorded both to larvæ and pupæ, and seems to be necessary for pupal development—in striking contrast to the bees and wasps, where the eggs are never touched by the workers, and the insect never leaves its little cell until it emerges as a perfect imago. The growing ant-grubs are fed by the workers, either with cut-up insect-meat, or in all higher forms by liquid regurgitated from the crop. Strange to say, the larvæ void no fæces, and are, indeed, incapable of doing so, since their stomach does not open into their intestine. The communication is only established just before pupation, and then all the accumulated fæces of larval life are extruded as a single large pellet. This is, perhaps, an adaptation for making easier the task of the workers in keeping the nest clean.

The grubs are regularly washed by their nurses, but this licking, though undoubtedly conducive to cleanliness, springs largely—as we shall see later—from greed on the worker's part. The full-grown grubs spin themselves cocoons, and in this guise are often miscalled "ants' eggs." Finally comes emergence to the unchanging adult state. Here ants once more illustrate the general rule that biological progress goes hand in hand with the greater dependence of the young; almost alone among insects, they require help, or at least are helped, out of their prisons. The adult neuters first help by biting holes in the cocoon; but the insect which then appears is still so far from independence as to merit the special name of a *callow*. It is not fully pigmented, and is still enclosed in what looks like a shirt, but is really its final moult. This is pulled off by the nurses. "When we see how gently this is done," says Büchner, "and how the young creature is then washed, brushed, and fed, we are involuntarily reminded of the nursing of human babies."

Lord Avebury made some interesting observations on the delegation of different tasks to different individual workers. This he did by making hourly observations every day for three months on a small artificial nest, in which the workers had been marked so as to be individually recognized. The colony was fed by being given honey at a definite spot outside the nest. The observations were made during the winter, when not much food is required. For over two months the honey was visited—with a few casual exceptions—by three workers only, which thus acted as sole foragers and transport workers and fed the rest of the colony by regurgitation. At the end of this time he imprisoned one of the three, and on the same evening another ant came out to the food. This new forager continued regularly at its task until after two days she also was imprisoned. Two days later a new forager appeared, joined a few days later by another. In another nest the same thing happened; but here none of the original foragers were imprisoned, and accordingly continued without change for the three months of the experiment.

How this division of labour is determined is not clear. The beautiful studies of von Frisch on bees, based on the same methods of individual marking, patient observation, and experimentation employed by Lord Avebury, have revolutionized our ideas of bee life. It is certain that an equally rich harvest of knowledge and interest awaits anyone —for the work can be carried out by an amateur just as well as by a professional biologist—who is willing to devote himself to a full study of marked ants, and thus to record the history of a single colony from the start.

It may take several years before a colony is adult; and, even when the swarms of new males and females are discharged, the old colony will continue. For one thing, the old queen may live ten years or more—seventeen-year-olds have been recorded—and will continue—still by means of her single original store of spermatozoa—to produce fertilized eggs until her death. Then, too, in many ants, some of the daughter queens regularly return to the nest after being fecundated, and, since the queen ant, unlike the queen bee, is never hostile to other queens of her own species, the nest comes to have a multiplicity of egg-laying queens, and so becomes potentially as immortal as a human nation. If such a colony continues to grow it will reach an inconvenient size, its food-needs outrunning its communications. When this happens new nests may be formed, just as new settlements were formed by the Greek cities, a band of workers with one or more queens leaving the old home to found a new one. Sometimes the new home is not far from the old, and then a federation of colonies is formed, differing from a number of separate colonies in the fact that all the workers are on friendly terms, and may pay visits to other nests within the federation.

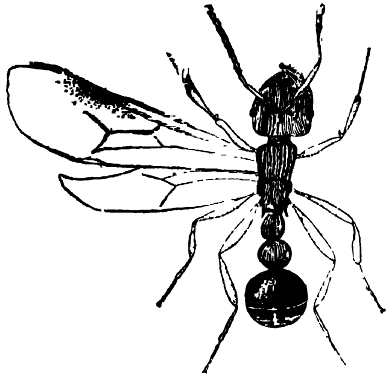
When a solitary queen founds a separate colony, on the other hand, the workers of this colony will exhibit hostility to those of all other colonies of the same species, including that which gave birth to their own royal founder. It seems probable that the friendliness or hostility of the workers to other ants of their own species depends on smell, each nest having some subtle "nest-smell" which is caused by each of its inmates. This smell-based friendliness may be extended to ants of other species and even to other insects. Not only must the mixed colonies of the slave-makers and the parasitic ants (Chapter VII) obviously be based on this acquired tolerance, but mixed ant-colonies may be artificially built up by human agency. Miss Fielde, following up some work of Forel, gave to one species of ant the pupæ belonging to another species of ant. When the alien workers hatched out they were accepted as part of the colony. Not only this, but they later showed marked hostility to their own blood-sisters who had been left to grow up in their own nest. Smell is thus to the ant what national traditions are to us—the basis of patriotism; and this patriotism, again as with us, can override the ties of blood and force relatives to fight against each other. In both cases the same end is secured—the subordination of the individual unit to the social unit of which he, she or it happens to form part: but the means are different.

The mixed colonies to be found in slave-making ants always consist of two quite closely related species. This is, in the main, due to the fact that the rearing of the young is a complex and delicately adjusted process, so that the needs of the larvæ of one kind of ant could scarcely be met by the instincts of the workers of some very different species. When, however, this difficulty is eliminated, as in Miss Fielde's experiments, by inserting full-grown larvæ into a strange nest, it is observed that smell covers a multitude of differences, for she could thus found compound nests even with two species of widely separated sub-families. The nest-smell doubtless also envelops in its protective mantle most of the many ant-guests, other kinds of insects which live dependently in the abodes of ants; but this we will consider later.

As regards caste and sex, all ant-species possess at least one sterile caste, the workers, in addition to fertile males and females. Anatomy reveals that the worker is a sterilized or neuter female, in whom may be distinguished rudimentary ovaries and oviducts. It seems certain that the difference between female—whether fertile queen or sterile worker—and male is determined, as in bees and wasps, by fertilization or the lack of it. Fertilized eggs produce females, unfertilized eggs produce males; and the control of sex-determination is exercised by means of the tight sphincter of muscle which in the queen's body surrounds the orifice of her purseful of sperms. If this is opened as an egg passes over the aperture, one or a few sperms pass out, and fertilization occurs; if it is kept shut, the egg remains unfertilized and male-producing. We know very little of what influences the queen ant to open or close this destiny-determining circlet of muscle. The differences between neuter and queen appear, again as in most other social insects, to be determined by differences in the quality of food given to the young larvæ, but here once more we know more of detail in bees than in ants. What causes the difference between winged and wingless queens or males, when both forms exist, is not yet known.

The fact that the differences between male and female are determined by heredity, those between queen and neuter by subsequent treatment, is shown by a study of the occasional mosaic monstrosities which occur when one-half or smaller area of the body is of one type, the rest of another type. Now, combinations are known of male part with queen part, of male with worker, and of male with soldier; but never of queen with either worker or soldier. All such monsters (called *gynandromorphs*) are to be explained through some abnormality of fertilization, presumably through the sperm entering only after the egg has begun to divide, and uniting with the nucleus of one only of the two or more cells produced.

Ants which partake of the nature of both queens and neuters do occur; these, however, the so-called pseudogynes, are never mosaics, but intermediate in every part. They seem to be the result of an alteration of diet in the middle of the grub's



(*a*) A GYNANDROMORPH ANT (p. 34). Its left half is male, its right half worker (sterile female).

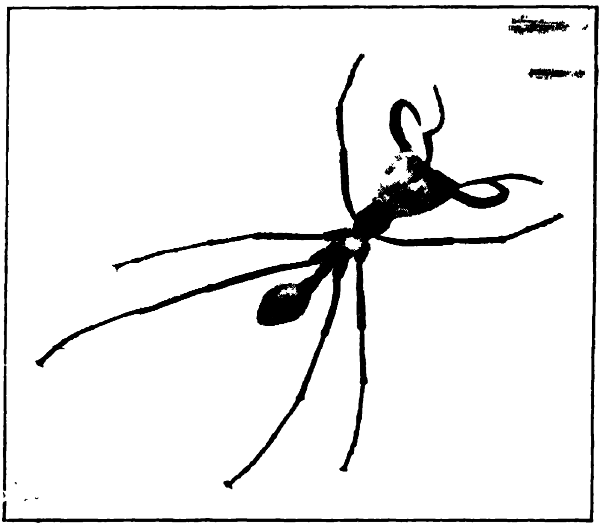


Photo by Martin Duncan

(*b*) AN EXAMPLE OF SPECIALIZATION (p. 80). A soldier neuter of Eciton, a wandering driver-ant, with long legs for rapid running, huge sickle-shaped piercing jaws, a large head enlarged to accommodate the muscles to work the jaws.

development. These pseudogynes, and also occasionally true workers, may lay eggs; but, as the parents have never been fecundated, the eggs can only produce males.

CHAPTER IV

FOOD-ECONOMICS

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FOOD-ECONOMICS

THE members of a human civilized community are tied together by economic bonds. Nobody but the cultivators of the soil can feed themselves by their own labour, and even they tend to specialize on one product, acquiring the rest of what they need by way of exchange. The agricultural population of Java, for instance, is so dense that it can only be kept alive by the import of rice, which is paid for out of the surplus of the exports of the more valuable coffee, rubber, and other vegetables which they cultivate.

With us, of course, there is a universal medium of exchange in the shape of money, and by the use of such a medium we raise our system of mutual exchange of services to a far greater level of flexibility than was possible by means of payment in kind or direct barter. The ants in an ant-colony are equally tied into a single economic whole; but the means by which this is accomplished are as unlike and, indeed, alien to those employed by man as is nest-smell to our methods of securing patriotism and the social subordination of the individual.

In the first place, the whole of the colony have, for practical purposes, but a single stomach. This arrangement occurs in such creatures as colonial polyps; but in them it is ensured by direct and permanent communication, the digestive cavities of each individual opening into a common communicating tube in the stalk. The ants have perforce had to adopt a less simple method. The food, after it has been reduced to a liquid soup, is passed down the narrow gullet, which pierces the nerve-collar in the head and traverses the whole thorax to open into the crop (or, as Forel, for reasons soon to appear, christened it, the "social stomach") in the fore part of the abdomen. The crop opens by a complicated valve into the true stomach, which in turn leads into the small intestine, and so *via* the large rectum to the anus.

When a worker has had a good meal, only a fraction of the partially digested food stored in the crop reaches the stomach and intestines, to be absorbed by the animal itself; most of it is distributed to other members of the colony, who solicit it by protruding their tongues and stroking the fortunate one with rapidly vibrating antennæ. On this, a drop of the food is regurgitated from the crop and passed into the other's mouth. The proof of the pudding is in the regurgitation. If an ant be allowed to gorge itself on syrup stained, say, blue with an aniline dye, the colour will show bright through her abdomen, and, as she distributes portions of it here and there among her fellow-citizens, and they repeat the process, the abdomens of almost every individual will become faintly tinged with blue. The collective stomach of the colony has been fed.

The food-interrelations between workers and larvæ are even more remarkable. The larvæ recapitulate a less specialized past in having a simpler gut, without a "social stomach," and in being able to deal with solid as well as liquid food. Many of them have a number of spines and roughened ridges near the base of their jaws. These when rubbed against one another possibly generate shrill sounds which, like a baby's howling, may serve to attract their nurses' attention. The remarkable facts elicited notably by Roubaud and by Wheeler both in ants and wasps show that the grubs, after being fed, secrete some liquid which the workers eagerly devour. In wasps and many ants this liquid is a specially sweetened saliva; but the majority of ants exude a fatty substance through their cuticle. In one sub-family of ants the larvæ are provided with extraordinary appendages which secrete a substance of this kind in more concentrated form, and are, one presumes, easier to suck.

To quote Wheeler's words: "Although these various substances are produced in very small quantities, they are of such qualities that they are eagerly sought by the adult ants. This explains much of the behaviour which has been attributed to maternal affection on the part of the queen and the workers, such as the continual licking or fondling of the larvæ, the ferocity with which they are defended, and the solicitude with which they are removed when the nest is disturbed. In other words, a decidedly egoistic appetite and not a purely altruistic anxiety for the welfare of the young constitutes the potent 'drive' that initiates and sustains the intimate relations of the adult ants to the larvæ, just as the mutual regurgitation of food initiates and sustains similar relations among the adult workers themselves." This payment by the larvæ for services rendered, Wheeler has christened *trophallaxis*, or exchange of foodstuffs. Thus, if the ants' patriotism is based on smell, their economic and social stability is founded on taste. The two cementing principles are rather different, since the common smell merely envelopes the colony and binds it together, whereas in trophallaxis there is a real economic exchange and a true bargain struck, the larvæ presenting the adults with coveted substances, unobtainable elsewhere, in return for attendance and plenty of plain food.

Since the subject is of such vital importance, we may here diverge a moment to look at trophallaxis among the wasps, where it exhibits certain simpler and more clear-cut features. The substance offered by wasp grubs to their adults is always the secretion of the salivary glands, which have apparently lost all their digestive functions and now secrete an abundant sugary liquid entirely devoted to rewarding their nurses.

Roubaud describes the act of trophallaxis thus: "As soon as a nurse wasp has distributed her food-pellet, she advances with rapidly vibrating wings to the opening of each cell containing a larva in order to imbibe the saliva that flows abundantly from its mouth. . . . The wing vibrations of the nurse serve as a signal to the larva which, in order to receive the food, protrudes its head from the cell. This simple movement is often accompanied by an immediate flow of saliva. But if the secretion does not appear, the wasp seizes the larva's head in her jaws, draws it towards her, and then suddenly jams it back into the cell, into which she then thrusts her head. These movements involve the stimulation of the larva's mouth, and force it to secrete its salivary liquid."

The nurses may return three or four times to obtain this secretion after they have fed their charges but once. What is more, the larvæ are sometimes exploited, and, by means of the curious handling just described (which appears to be instinctive, in origin at least, on the part of the adults), made to secrete saliva without any compensatory gift of food. This, which amounts in the wasp's economic system to thieving, is practised almost entirely by workers which have just emerged, by the queen, and by males. It is interesting to find that this secretion can be artificially induced, either by touching the larvæ on the borders of their mouths, or by simulating the effect of the nurses' vibrated wings by whistling near by. "It is only necessary to whistle loudly or emit shrill sounds near a nest of Belonogaster to see all the larvæ protrude their heads at the orifice of their cells."

J. B. S. Haldane has pointed out a further biological meaning in the wasps' trophallaxis. Most of the food actually in the blood-stream of a mammal is utilized as fuel, in the form of sugar. The nitrogen-containing amino-acids derived from meat and other proteins are employed for tissue repair, but only quite small quantities are needed for this, the remainder being broken down into sugar further utilizable as fuel, and waste nitrogenous substances like urea. The growing puppy or human child, on the other hand, utilizes a much greater amount of its nitrogenous food, since it has to build tissue as well as repair it. In these respects, insects are like mammals, but more so, since the cold-blooded, sluggish grub requires relatively less fuel. Thus trophallaxis as practised by wasps is not only a system of services and rewards—it also ensures a more economical utilization of the food. As Haldane says, "When a worker comes to feed a grub . . . the grub thanks it by secreting a drop of fluid containing sugar for which it has no use, but which is valuable fuel for an active insect" (and one, we may add, which is no longer growing).

The bees, curiously enough, appear to lack all trophallaxis between grub and adult, nor is there any transference of food from one worker to another. The first point may be accounted for by the facts mentioned by Haldane. The food of bees consists mainly of the sugar-containing nectar, transformed into honey during its sojourn in their crop, and the pollen, or bee bread, rich in protein. The adult bees require no extra carbohydrate, since they obtain it directly in their ordinary food; the grub can have its nitrogenous and non-nitrogenous rations exactly dosed. The lack of mutual feeding by the adults can be equally easily accounted for: the bees have produced an artificial substitute for the "communal stomach" of the ant colony, in the shape of their cells of pollen and honey. The workers regurgitate their gathered stores into these instead of into other workers' mouths; and, since some of them are always left open, home-staying bees can always draw upon them when hungry.

Finally, the termites have developed very extraordinary systems of communal food exchange, which will be discussed in a later chapter.

CHAPTER V

ANT SENSES

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THE senses of ants are of considerable interest. Sight can never be very acute, as the compound eyes have few and widely diverging facets. The simple eyes or ocelli, present in almost all forms, can only serve for extremely near vision, or perhaps merely for distinguishing light from darkness. The driver ants, for all their ferocity and active migrations, are wholly blind. It is of some interest that some ants, at least, are sensitive to a certain range of ultra-violet light unperceived by us.

In ants the only sense organs of any delicacy of discrimination are the antennæ. These mobile organs explore the environment with a combination of smell and of touch in a way which we, with our organs of smell fixed within our skulls, can scarcely imagine. Smells for us are without form and void. But ants can undoubtedly distinguish the *shape* of all such smells as are being given off by definite bodies of small size, and they must have a composite notion of such a body in terms of smell, of colour, form, and shading derived from sight, and solidity derived from touch. In the battles between different colonies of the same species of ant, friends cannot be distinguished from foes by distinctive markings or uniform, nor are there any battle-cries. It appears that a touch of the antennæ at once decides the point.

An obvious problem of ant biology is to know how ants find their way back to the nest after long expeditions into the surrounding country. Once well-marked trails have been established, the track itself and the smell adhering to it simplify matters a good deal. But what of solitary workers exploring off the beaten track, and their power not only of returning to the nest, but also of bringing back a band of other workers to any source of food they may have discovered?

As a matter of fact, most species of ant seem to employ three or four different methods in finding their way. To a slight extent they utilize what to us is the most important method—that of orientating themselves with regard to objects in the landscape. Wherever there exists a trail over which they or other ants have gone, they rely largely upon smell. Smell, however, cannot very well tell them much about direction. Although Bethe put forward an elaborate theory in which he supposed that an ant, by means of its power of detecting the shape of smells, could distinguish in which direction ant footprints were headed, he had to make the unlikely supposition that the ants travelling out from the nest imparted a somewhat different smell to their traces from those coming back! Recent workers, however, following up a clue left by Lord Avebury, have been able to show that this is not so, and that the ants are guided in their direction by the direction of the light falling upon them. If, for instance, a solitary questing ant is imprisoned under a box for three hours, and the box then taken off, it sets off in a direction which deviates from its original line by the same angle through which the sun has travelled during its imprisonment—in this case 45 degrees. This it will do whether it had been travelling directly towards or away from the sun, or at an angle to its light. In artificial nests the ants can be completely tricked by moving the source of light. Apparently, on days which are overcast, the ants can still orient themselves approximately in relation to the part of the sky most strongly illuminated; but more experiments are needed on this point.

Finally, the ants must have some sort of sense of distance, for when an ant has been tricked, by being kept prisoner for a time, into following a false direction on its homeward way, it stops its straight, unhesitating march when it has travelled a distance, which, had it been moving straight homewards, would have brought it to the near neighbourhood of the nest, and begins to quest about in every direction. Apparently this faculty depends on some utilization of the kinæsthetic or muscular sense, the number of leg-movements being more or less accurately registered. It is certain that a similar mechanism is at the basis of the power of rats and other animals to learn a maze. Whatever the precise machinery at work, there is no doubt that many animals do possess some such automatically registering pedometer as part of their equipment.

Many are the stories of ant intelligence. Most of them, however, smack much more of trial and error, or of adapting instinct slightly to unusual circumstances, than to intelligence properly so called.

Some ants are undoubtedly very stupid, judged by our standards. Lord Avebury found that the little ants which he kept in captivity could not learn to build up earth into a pile an eighth of an inch in height in order to get at some honey which they could smell and see just out of reach, nor to perform a number of equally simple mechanical acts which would have secured them food or access to their larvæ.

On the other hand, there are trustworthy accounts of driver ants bridging streams by each worker seizing a twig and then forming a living chain-bridge across the water, over which the rest of the army can cross; and Bates himself records how the path of some South American ants lay across a tram-line, and how, after a large number had been squashed by the tram, they made tunnels under the rails. When Bates stopped up these tunnels the workers refused to cross the rails, but waited until new tunnels were made. Cardinal Fleury communicated to the great Réaumur his observations of how ants surmounted a girdle of bird-lime smeared round the trunk of a tree by laying a road of earth and small stones across it; and the fact has been corroborated in recent years, one observer stating that he had seen ants, trapped on a tree by a band of tar, bridge the obstacle with their own ant-cows! Others in similar predicament have been known to reascend the tree and drop from the branches, although Lord Avebury's ants (perhaps because they belonged to a species with very poor sight and less roving habits) refused to let themselves drop through half an inch.

Some of the building activities of ants, too, display definite intelligence in the sense of the adapting of means to ends, but there, too, instinctive foundation always remains and is larger than the superstructure of intelligence. The enormous gulf between the intelligence of ants and our own is most readily realized by reflecting that no ant receives any education. The larvæ are mere machines for growing up as quickly as possible, with the most rudimentary sense-organs and no limbs; even if they were taught, which they are not, their capacity for profiting from the instruction could not very well transcend that of an earthworm.

The pupæ are shut away from the world in their cocoons, busy with the task of transforming their whole organization from that of helpless grub to winged six-legged creature. Finally the adults, once emerged, can set about performing all their complex tasks without the least instruction, as is shown both by observation of young nests and by experiment. They find the food proper to the species, they build the right kind of nests, they tend the young in one particular way. They may improve as the result of practice, or may have new habits thrust upon them by necessity and experience; but there appears to be no way in which tradition can be communicated from older to younger workers, and certainly no way in which it can be transmitted to a new nest. In respect of education and tradition, even the highest of social insects is below the level of a mammal such as the dog.

All ants are extremely cleanly animals. Not only, however, are they cleanly with regard to their own persons, but their social nature prompts them to mutual assistance in matters of the toilet. We may take McCook's account of the operation in the fungus-gardener Atta: "We take a couple; the cleaner has begun at the face, which is licked thoroughly, even the mandibles being cared for. . . . From the face the cleaner passes to the thorax, thence to the haunch, and so along the first leg, along the second and third in the same manner, around to the abdomen, and thence up the other side of the ant to the head. . . . The attitude of the cleansed all this while is one of intense satisfaction, quite resembling that of a family dog when one is scratching the back of his neck. The insect stretches out her limbs, and as her friend takes them successively into hand, yields them limp and supple to her manipulation; she rolls gently over upon her side . . . and with all her limbs relaxed presents a perfect picture of muscular surrender. . . . I have seen an ant kneel down before another and thrust forward the head, drooping, quite under the face, and lie there motionless, thus expressing . . . her desire to be cleansed. I at once understood the gesture, and so did the supplicated ant, for she immediately went to work."

Ants, like other higher insects at least, require sleep. The exposition of sleep may come on at any time of day, and its duration, in those species where it has been timed, averages some three hours. They may choose a depression in the soil as bed, and there lay themselves down, with legs drawn close to the body. When asleep, they may be stroked or tickled without awaking, though a sharper tap rouses them at once. When waking naturally, they behave in a way startlingly like that of mammals or our proud human selves. The head and then the six legs are stretched to their fullest extent, and then often shaken; the jaws are strained open in a way remarkably reminiscent of a yawn. One interesting observation made by McCook on an American harvesting ant with great difference in size between the workers and soldiers, was that the soldiers sleep longer, and also more heavily, being much less easily awakened!

Some observations indicate that ants have reached that high state of mental development at which play appears. The sport generally consists in mock fight between the workers of a single colony, the ants behaving just like dogs when they play at fighting. They may also pursue each other, again like puppies, or like children playing tag.

This brief account of some of the general habits of ants may fittingly conclude with a reference to the way in which their bodies are disposed of by the community after death. Some of the older naturalists gave the most circumstantial accounts of regular ant funerals, with corpses borne by workers two and two in procession, and finally interred in separate graves. It appears that imagination had here a little outrun fact; none the less, the fact is interesting enough. Most ants are extremely anxious to dispose of any corpses, and if kept in a small artificial nest will wander round with their burdens, often for days, searching for a suitable spot. In nature, the usual cemetery is simply the communal refuse-heap, so that it is probable that the corpses are merely regarded as so much refuse, and the apparent solemn burial of the dead turns out to be only a special case of the ants' passion, doubtless implanted by natural selection on account of its utility to the colony, for keeping the nest tidy. It has, however, been asserted that the slave-making *Formica sanguinea* has separate places of disposal for the corpses of its own species and that of its slaves.

CHAPTER VI

WAYS OF LIFE AMONG ANTS

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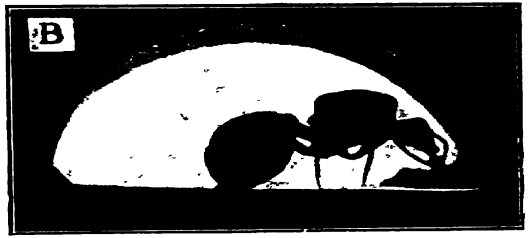
ANTS are essentially terrestrial creatures, though a few have secondarily taken to tree-life. Though of world-wide distribution, they are pre-eminently inhabitants of dry or desert regions. In structure, they bear witness to definite relationship with the Scolioids, a group of solitary wasps, and there can be little doubt that they have originated from a ground-nesting wasp of this type which took to social life with loss of wings in the workers, but not in the sexual forms. Their abundance in arid lands suggests that this development first took place in one of the long arid periods of the northern hemisphere, presumably in the Trias or Lias of the Secondary epoch.

At the beginning, all the workers were doubtless alike, and not markedly dissimilar from the queens. But terrestrial life and social specialization gradually rendered the ant neuter more unlike the queen than in any wasp or bee. Meanwhile, the average size of the colony doubtless increased.

away devourers. But in most cases the ants take advantage of the much more abundant supply afforded by the various little sap-sucking insects —aphids, scale-insects, leaf-hoppers, and the rest. These wasteful creatures only use a fraction of the sugary solution which, with their sharp proboscis, they are imbibing all day long; the remainder exudes at their anus. The ants, however, always the exemplars of frugality, have not tolerated this waste. They either lick up the excreted "honey-dew" from the surface of the leaves, or "milk" the animals by stroking them with their antennæ. Finally, some species actually domesticate these ant-cows; and others store the honey-dew against the dry season—in an extraordinary way of which an account will be given later.

Then in some Myrmicines, the pastoral stage has given place to the agricultural. A half-way house is reached by the so-called harvesters, which collect the seeds of grasses and store them in regular granaries, although, contrary to early belief, they never sow seeds for a new crop, and so do not fully merit the name of agriculturists. But some other genera of the same sub-family practise a real horticulture, growing fungi for food, and attending to the growth and reproduc-



Photos by Dr. Carlos Bruch, from Forel's "Monde Social des Fourmis." (Librairie Kundig, Geneva)

(*a*) THE BEGINNING OF A FUNGUS-GARDEN (p. 70). A mated queen of the parasol ant Atta has founded a new nest, in which she has laid four eggs and has started a fungus-garden. The fungus threads on the surface are clearly visible.

(*b*) TENDING THE FUNGUS-GARDEN. The Atta queen is manuring the fungus-garden shown in (*a*) with her own excrement.

tion of their vegetable plots as assiduously as any human gardener.

Finally, as a strange overshooting of the mark, a specialization which eventually leads downhill, there are the thieving, slave-making, and parasitic ants. There exist ants which are occasional brigands; others which are persistent thieves, and some which are servile parasites. In both Formicines and Myrmicines, the subtler form of parasitism which starts as slave-making has been evolved. Some are temporary slave-makers, others must live with slaves all their lives, and still others have completely lost their worker caste, the queens and males living as mere parasites on their slaves.

There is no reason whatever to suppose that the ant-type will not continue to flourish through future geological periods as admirably as it has done in the past. As a type, it most efficiently fills a definite niche in terrestrial life. A few species will doubtless be exterminated by man, some deliberately, others as the unforeseen result of agriculture and other human activities; but the type as a whole will be protected by its small size, subterranean habits, and adaptability. New species and new modes of life will doubtless come into existence, but the type itself will persist essentially unchanged, as a witness to the biological success of social life utilizing the efficient machinery of insect structure and held together by firm and elaborate instincts.

After this brief general sketch of ant evolution, we may turn to some actual pictures of ant-life, as led by different species of this strangest of all earth's little peoples.

MARKET GARDENING ANTS

Let us look first at Atta, chief among ant-gardeners. In woods from Texas to Brazil there may occasionally be seen processions of ants, following well-worn trails often a hundred yards or more in length. Those going in one direction are empty-jawed, and walk on one side of the road; those going the other way keep to the other side and carry a piece of green leaf. The piece of leaf is often so large as to hide the animal that carries it, and has led to these creatures being called parasol ants. The leafless workers are on their way up trees; there they cut out their green "parasols" with their jaws; and thence carry them back to the nest, or let them fall one after another to the ground, there to be picked up by another gang.

The nest may be enormous, a veritable subterranean city, the débris of its excavations piled into mounds ten or twenty feet across. The mound of the common Brazilian parasol ant, *Atta sexdens*, may run to 265 cubic metres of earth, weighing many hundred tons, and may shelter over half a million individuals.

The neuters of Atta cover a great range of size, from the huge-headed soldiers down through large and medium and small workers to the tiny *minimæ*. The soldiers defend the nest, and police the bands of medium and large workers who make it their business to clip the leaves.

In the nest the leaf-pieces are cut into smaller bits and built up into beds on the floor of the large subterranean chambers which other workers have previously excavated. These beds are then handed over to the smallest workers, who work only underground, though they are said to come up occasionally to play about in the light and air. On the beds of decaying leaf grows a white network of fungus: this is tended by the smallest workers, who treat it by some unknown method which makes the threads produce clusters of small spherical swellings. These miniature white cabbage-heads are bitten off and used by the ants as the staple food both of themselves and their young. The ants seem very careful about the proper ventilation of the gardens, and Bates describes them as opening or closing some of the numerous holes leading to the surface from the fungus-chambers, according to the conditions of moisture and temperature. They are also careful not to bring in pieces of leaf if they are too wet, but leave them near the entrance to dry. Grass is apparently unsuitable for fungus-beds. In spite of this, ants are occasionally seen carrying bits of grass into the nest; but these are always thrown out again after a time.

Every species of Atta grows a different kind of fungus, and, what is more, weeds out any other which may start to grow in the nest. The fungus-heads are artificial productions of the ants' gardening just as definitely as are crisp and white celery stalks the product of the treatment the plant receives from man: they do not appear when the fungus is grown in the laboratory. Indeed, they are much more modified than celery, for the fungus-threads are really the mycelium, or "spawn," of a regular mushroom. So long as the ants' cultivation continues, the fruiting mushroom structure never appears, but in abandoned nests they are sometimes found pushing up. Several distinct genera of fungus have thus been domesticated by the Atticine ants, including one which is not related to the mushrooms at all, but is more like yeast.

It is probable that the Atta workers manure the gardens with their own excrement. Certainly some related forms use the dung of caterpillars and other insects as the substratum for the fungus, in place of leaves. Others suspend the fungus-beds from the ceiling.

The transference of the precious fungus from colony to colony is effected by the queens. All ants possess in the forepart of their mouths a pouch, the so-called infra-buccal pocket. Into this, in the ordinary ant, are swept first the more solid food-particles after they have been masticated by the jaws, and also, strangely enough, the combings and scrapings of the ants' toilet. These latter are combed off her legs and antennæ by means of a pair of opposable combs on the fore-leg, and licked off the rest of her body by the cleanly creature's tongue. The pellet in the pouch is moistened with saliva, which dissolves out any available food, and when it has reached a certain size it is thrown out. No adult ant thus swallows anything but liquids.

The pocket is utilized by the parasol ants for the inoculation of new nests with fungus. The virgin queen, before leaving the nest on her nuptial flight, takes a hearty meal—of fungus, of course. Threads of the mycelium, together apparently with some of the leaf-soil, are packed into her infra-buccal pocket. After she has mated, cast her wings, and constructed a small underground room as beginning of the future nest, she spits out the pellet on to the floor. The fungus naturally begins to grow, and the queen tends it with the greatest care, manuring it with her fæces, and even breaking up some of her own eggs to furnish more "soil." She uses the garden as a nest for other eggs; the larvæ from these hatch out, feed on the fungus, and turn into workers. These, untaught, break out of the chamber, raid trees for leaves, and take the charge of the garden off the queen's shoulders. Thus an extremely slight modification of an old-established habit suffices to ensure what at first sight seems to us no simple task—the transmission of the fungus-vegetable to new nests.

It is interesting to find that the cast pellets of most sorts of ants almost always contain fungus-spores. What is more, most ants have a regular refuse-heap in or near the nest, and many species make a practice of voiding their pellets here, just as man and several mammals, like the rhinoceros, prefer to defæcate in definite spots. This refuse-heap affords favourable conditions for the germination of fungi, and in point of fact in some species of Crematogaster not only does an abundant crop of fungus-threads grow on the refuse-heaps, but the ants actually use this as part of their diet. And from an accidental state of affairs such as this it is not a very large step to that found in the true fungus-growers. Thus even such a surprising activity as deliberate vegetable-gardening can have had a comparatively simple and intelligible evolution.

HARVESTING ANTS

It was *Messor barbarus*, one of the harvesting ants, to which Solomon referred when he wrote his celebrated advice to the sluggard (Prov. vi. 6). It was for many years believed that these creatures not only stored grain but actually sowed it in definite fields in order to raise a new crop. In view of what has occurred with the fungus-growers, this would be quite possible (save that it is more difficult to think of the practice arising when months instead of days or hours must elapse before the new crop appears); it merely happens not to be true. These ants often clear a considerable area round their nests; and on this bare area grasses may sometimes be found sprouting. However, this is not due to any deliberate sowing by the ants, but only to the germination of accidentally dropped seeds.

The harvesters are all inhabitants of desert or semi-desert regions. Not only is insect-food scarce, but there are long periods of drought in which both active plant and animal life is almost absent. Thus the ants find in seeds a welcome addition to their diet, and also a food which can be stored against a dry season. When they can find insects, they still will eat them readily enough. Several of these ants have neuters ranging from small workers up to huge-headed "soldiers." These latter, although they are precisely similar in general structure to ordinary soldiers, have taken upon themselves a new and different function. The larger and harder seeds are broken up by them with their enormous mandibles, and so made available to the rest of the colony.

In some cases—for instance, the Myrmicine harvester (*Pheidole instabilis*) from Texas—there is a complete and continuous gradation between the largest soldier and the smallest worker, as in Atta and some of the driver ants. When the whole series is examined it is seen that the differences between the various forms are differences of proportion: the larger the neuter, the relatively larger head-organs does it possess. What is more, whenever in such forms the weights of head and body are taken, it is found that they obey a simple mathematical relationship—head-weight is a function of rest-of-body weight raised to a power; and this would imply that head and body grow at different rates, but rates which always bear a constant ratio to one another, like two sums of money accumulating at different rates of compound interest.

These facts give us a probable clue to the origin of the sub-castes among ant neuters. There is always some variation in the adult size of insects, due to the quantity of food available to the larvæ. The social insects are no exception to the rule; one of the most striking examples is given by the Humble-bee, in which the first-hatched members of a new nest, owing to the overworked queen not being able to provide a great deal of food, are always smaller than their mother—sometimes scarcely larger than house-flies—although they are not neuter. The neuters of all ants vary in the same way, the range of size being much greater in some species than in others. In many cases the difference is one of size alone, the proportions of parts remaining the same. Even here the variation may be turned to advantage, very small workers being suited for delicate work in the nest, very large ones for heavy jobs in transport or construction; and, if advantageous, the condition would readily be brought about through the nurses giving abundant food to some larvæ, very little to others.

But growth of all parts of the body at the same rate is really only a special case; in reality, different parts usually grow at slightly different rates. The jaws of ants are their main tools and weapons both. Thus the advantages of size-variation would obviously be intensified if the large individuals had also more powerful jaws—and therefore, because of the muscles required, larger heads—and this would be insured if in the pupa the rate of growth of the rudiments of the adult head were greater than that of the rest of the body. Not much difference is necessary; the head's growth-rate need never be twice as great as the body's to produce soldiers which are almost monstrous.

Thus the whole gamut from super-soldier to *minima* workers one-fiftieth their bulk could be produced by a combination of two well-known principles—variation in imago-size dependent upon the amount of food received by the larva, and the differential growth-rate of one region of the body. The growth-rates are given by heredity; once they are established, all that is needful is that the worker-nurses should vary the food-supply of the grubs. The view that this has actually been the course of events in ants is supported by the fact that whenever new nests, of species with polymorphic neuters, are founded by single queens, the first brood consists only of small workers and never contains soldiers; for the same reason, one presumes, that the first brood of humble-bees are small—because the queen has not time nor energy to feed them up.

In the genus Pheidole, some species, like *instabilis*, exhibit the complete gradation we have just studied; but the great majority possess nothing but soldiers and tiny workers. This must be due to a further specialization of the nurses' behaviour—they either feed their charges to the fullest extent, or keep them on a definite scale of reduced rations. The result is a sharpening of the division of labour—a specialization perfectly analogous to that between the different tissues of the body.

Ant-Cows

It was Linnæus who first christened plant-lice the ants' cows; and the phrase is perfectly legitimate. The domestication of plant-lice has reached such a pitch among certain ants that the masters—or, rather, mistresses—collect the "cows'" eggs in autumn, keep them through the winter in their own nests, tending them like their own, and in the spring, when they begin to hatch, plant them out in their pastures, distributing them over the roots, leaves, or stems of neighbouring plants. For instance, *Lasius americanus*, one of the commonest ants of the United States, distributes plant-lice far and wide over the roots of Indian corn, while in the European *Lasius flavus* Lubbock found them planting out eggs on to daisy-plants; and others take their charges high up on to trees. Other ants keep their dairy beasts browsing on roots in specially constructed rooms underground, or even build sheds or barns over them as they suck the juices of leaves high up on shrubs or trees. These sheds are sometimes connected by long, covered ways with the nest. Care is usually taken to have the doors too small for the cows to get out, though big enough for the ants. All such herd-masters practise the "milking" of their insects, stimulating them to defæcate by stroking their bodies with their antennæ. Darwin and others have tried to imitate this by stroking aphids with a hair, but this is of no effect; yet even very young aphids respond at once to the blandishment of the ants' feelers, though, in the absence of this stimulus, they hold up their secretion for long hours.

When the ant-cows are kept permanently underground, as in plant-lice and mealy-bugs tended by *Lasius americanus*, they become snow-white—not, as with our white cows or horses, through positive selection, but through the direct or indirect effect of the lack of light. What is more, their herd-mistresses, never needing to come above ground for their food, are pale yellow in colour, and have become almost blind, with vestigially minute eyes.

As we have seen, this dairying life has grown up naturally enough. It is based on the fact that the sap-sucking insects utilize only a small portion of the sap they pump up from the plant tissues, but void the major part of it. From licking up this sweet liquid, so agreeably made available to the ants—for their own jaws are useless for sap-extraction—to waiting for the actual time of voiding is a simple step enough, and the stroking of the "cows" to speed up the appearance of the drop is another. The ants' invention of milking other insects is certainly no greater, as an evolutionary advance, than man's invention of milking other mammals.

Just as man's agriculture, whenever it becomes at all systematic, is extremely deleterious to most other organisms, what with the felling of forests, the draining of marshes, the killing of beasts of prey, the banishment of so many birds which need cover or solitude; so the dairying propensities of the ants constitute one of the most harmful of all their activities. So numerous are the species engaged in the protection and often in the active dissemination of sap-sucking insects that a heavy toll is laid on plants, and man's efforts to keep his crops, flowers, and fruit-trees clean of these vitality-sapping pests are, in large part, rendered vain.

HONEY-POT ANTS

Just as the harvester ants must store the seeds on which they live to tide over the dry season, so, too, the honey-dew eaters of arid regions must find some method of storage. Liquid food, however, is not easy to keep. The honey-bee has solved the problem; but the honeycomb is the climax of a long and gradual evolution. The ants never adopted this type of storage method, and the sudden invention of a pot or bin with an air-tight lid is not simple when evolution is working mainly by instinct. The honey-ants have arrived at a different solution, which is unexpected to us, but natural enough in insects—they convert some of the workers themselves into storage vessels. These living honey-pots have an enormously distensible crop, and the foraging-workers in the season of plenty feed and feed them by regurgitation until their abdomen becomes swollen to a huge spherical bag, the plates of its skeleton eventually becoming isolated on a great area of tight-stretched elastic skin. The "repletes," as they are called, are quite incapable of walking, and remain suspended by their claws from the roofs of special chambers, in which a number of these "animated demijohns" hang side by side for months. In the dry season the ordinary workers stimulate them to regurgitate in the usual way, by stroking their heads, and so the whole colony is kept alive out of their capacious bellies.

This adaptation has been evolved independently in three sub-families of ants, always in desert countries. It is interesting to find that the single genus Pheidole contains species adapted wholly to harvesting and others wholly to this storing of honey-dew. It is not known whether the repletes are predetermined for their task by the possession of specially distensible crops. More probably the possibility is open to all workers, but only a certain proportion of their number have repletion thrust upon them.

THE LEGIONARY ANTS

The predatory habit has been carried to its farthest extreme by the Legionary or Driver ants, already mentioned. These dreaded creatures, with their destructive instincts, their nomadic habits, and the vast numbers of their hordes, remind us of the invading hosts of Huns or Tartars in our own history. But here again the fundamental differences between man and insect appear. The most restless of the Mongols was capable of settling down to a stable and civilized life. But the driver ants are for ever limited to their way of life by the iron hand of heredity. Their nomadism and their ferocity are permanent; their wanderings are barbarous invasions that never end.

Their blindness makes them more uncanny to us; but it is only one more instance of the subordination of sight to smell among ants in general. They usually exhibit great polymorphism among their neuters, the powerful soldiers attacking the largest prey—even horses and cattle are attacked and killed, when tethered—and rendering it available to the others; the small workers are equally ferocious and see to it that smaller creatures do not escape. The males, as usual, are winged; but the queens are permanently wingless, and grow into great egg-laying machines only excelled in bloatedness by queen termites.

CHAPTER VII

WARFARE AND SLAVERY

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ANTS are among the very few organisms other than man which go to war. Individual insects or spiders, fish or birds or mammals, fight each other for food or mates or breeding-sites; but this is not war. When a herd of wolves attacks a herd of wild horses, and the prey vigorously defends itself, this is a first approximation to war. But strictly the term should be confined to battles between armies of the same or closely related species. In ants there are all gradations from the pure predatism of such forms as the legionaries, against which no other ant defends itself, up through stages where the species preyed upon occasionally defends itself vigorously or even takes the offensive, to those of habitual warfare between closely allied species, and, finally, battles between different nests of the same species.

The best-known military activities of ants are those concerned with the raids of the slave-makers on the nests of the related species from which they wish to steal pupæ to be reared as slaves. The general biology of slave-making will be considered later; but the purely military aspects may be treated here.

In more peaceful species solitary workers scout about for food, and, after it is found, their return to the nest is followed by a large exodus of other workers to exploit the provisions. Similarly, the slave-makers' scouts go out in search of suitable nests to attack; and, when they return successful, all the neuters of the nest advance to the attack in a body. The Amazon slave-maker, Polyergus, forms in dense columns when near the objective, apparently searching for the scent. Such columns may be fifteen feet long, with breadth up to six inches, and the march, at an average speed of a yard a minute, may last an hour or more. The leading ants are apparently sniffing eagerly for the scent of the slave-species. When this is found they dash forward to the attack. Some slave-species fly at once. Others offer violent resistance; but they are usually driven to fleeing with as many larvæ and pupæ as they can save, and to pursuing the Amazons, when these retreat, in the attempt to retrieve some of their booty. The returning column of slave-makers, guided solely by smell, follows the precise route which it took on the outward journey.

Forel has seen a whole army of Amazons lose its way and fail to find its objective; when the way is very long they may, though headed correctly, turn back again, apparently as the result of fatigue. There seems to be no leadership in the human sense, but some ants often appear to be very half-hearted and need to be tapped with the antennæ of more actively inclined animals before they will advance. Halts are often made to let the column close up, and usually again when the van has arrived close to the objective.

The same nest may be attacked day after day until there is nothing left to steal, or the inmates move to a new site. One Amazon colony, watched every day for a month, was seen to send out forty-four raiding expeditions, of which twenty-eight were complete triumphs, nine gained a few pupæ, and seven were total failures.

In one case observed by Forel some of the colony of *Formica fusca* which was attacked defended the nest with great vigour, while others succeeded in carrying the great majority of the brood out of danger, upon which the Amazons gave up the attack and began retreating. The *fusca*, however, violently excited, poured after and pursued them, and were so successful in harassing them that the enemy released the slave-young they had captured, and got away by utilizing their superior speed. Such a defeat is exceptional. In this case it seems to have resulted from the front of the attacking column having come within sight of the defenders before they expected, and to the pause which then ensued while the rear was brought up being utilized by the *fusca* to man the nest thoroughly for defence.

Forel has also observed the attacked ants follow the slave-makers to their own nest, and launch themselves in hundreds in a vain assault upon it. The hostility of slave-making and slave-species is but a special case of normal prey defending itself. But different species of slave-makers are violently hostile to each other, and when they meet may wage battles as bloody as those against the slave-species. Finally comes the warfare in which the ants rival man, that where all the combatants are members of the same species. The Harvester ants seem to be the chief of such fighters, the accumulation of portable possessions leading, as with us, to cupidity and war. Such wars are fully as savage as those between the slave-makers and their victims, and may be very prolonged. One campaign between two neighbouring nests, described by

Moggridge, lasted forty-six days; another, observed by McCook, which took place in Penn Square, in Philadelphia, lasted nearly three weeks.

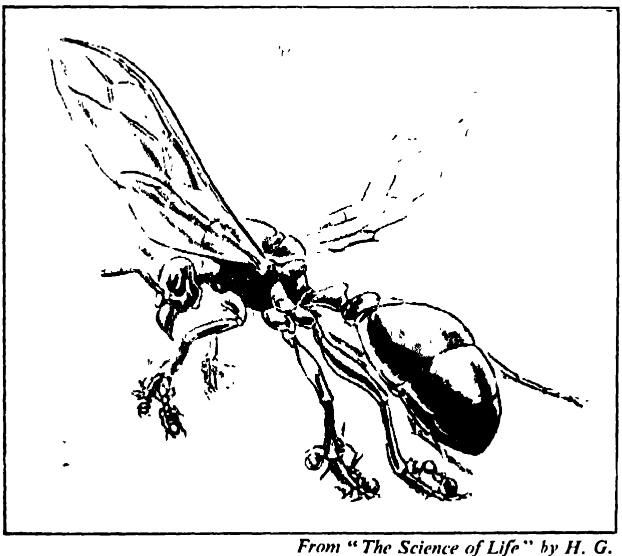
One of the commonest causes of war is the building of a new nest too close to an old-established one, the ants in them displaying a territorial instinct very like that of many birds; on other occasions, however, scarcity of food may lead to hostilities between two nests previously at peace with each other.

The fact that two species of ants constantly nest in close proximity is the first step towards the form of parasitism which has had the name of slave-making applied to it, for, as Wheeler remarks, "different ant colonies, even of the same species, are so hostile that their mere existence in such contiguity implies that one of the species is to some extent exploiting the other."

Some small ants live like brigands in dwellings close to the pathways of other ants, and snatch food from the returning workers, just as the skua compels the gull to disgorge its booty. The reason they are not attacked by their victims is not clear, but, as with the gulls and skuas, may lie in a difference in the disposition of the two species. Others, always of minute size, are permanent thieves. They make nests in the very walls of large ant or termite nests, and connect the galleries of the two dwellings by passages large enough for their own use, but far too small for their large neighbours to pay a return visit. An extreme adaptation to such a life is shown by Carebara, which steals from termites. The workers, in accordance with their mode of life, are among the smallest of all ants, while the males and queens are of more or less normal ant-size, and weigh over a thousand times as much. When the queen flies out on her marriage flight she takes a number of the little workers with her, clinging on by their jaws to the hairs of her legs. It has been plausibly suggested that this is an adaptation to the huge disproportion in size between the queen and the worker, since the queen could no more feed her pigmy offspring by regurgitation than could the ladies of Brobdignag have successfully given the breast to a normal-sized human baby, and needs neuter nurses from the first. As an example of the blind nature of ant behaviour, it may be mentioned that workers, at the moment of the nuptial exodus, attach themselves indiscriminately to males as well as to queens, in spite of the fact that all which happen

(*a*) HONEY-POT ANTS (p. 78). A number of "repletes" or workers, with their crops distended with honeydew, are resting on the roof of a storage chamber. Below, one of the repletes is regurgitating food from its crop to an ordinary worker.

(*b*) EXTREMES OF SIZE within a single ant-community (pp. 16, 90). A queen of the thief-ant Carebara setting out on her nuptial flight with a number of tiny workers clinging to her legs.



From "The Science of Life" by H. G. Wells, J. S. Huxley and G. P. Wells. (Waverley Book Co., Ltd.)

to take the male conveyances must die without fulfilling any useful function.

Occasionally weak, small ants live near the nests of large ones, merely, it would seem, to enjoy some protection from their powerful neighbours' proximity; and, at its highest, this relationship passes the low barrier which separates one-sided exploitation from mutual service, and assumes, on the instinctive level, the form of a true alliance. For instance, in tropical South America a large brown Camponotus and a small dark-coloured Crematogaster jointly inhabit a curious arboreal nest which consists of a tunnelled ball of earth built round a tree-branch. (Such tree-nests of earth are usually overgrown with a fine "garden" of epiphytic plants, but these appear to owe their presence merely to accident, and to play no part in relation to the life of the ants.) The small-statured ant-people inhabits the outer layers of the nest, and its neuters rush out in defence whenever the nest is disturbed. The larger species lives in the centre, and, though extremely formidable, only emerges if the danger is serious. There is thus a division of labour between the two species analogous to that which obtains between workers or small skirmishing soldiers and large, heavy-armed soldiers of one and the same species. Even in this case, however, the young of the two species are kept and tended separately, although the adults continue to utilize the military advantages of the alliance by foraging together.

What is, in one sense, a further step, has been taken by certain small ants such as Leptothorax, which, like many human parasites, get their living by making themselves agreeable. They make their galleries in the walls of Myrmica nests, but obtain their food directly from the Myrmica workers. This they do by creeping up on to their hosts' backs and licking away at their bodies and especially their mouth-parts. This titillation seems to please the Myrmicas, for they respond by regurgitating food for their little menials. These Leptothorax are thus in precisely the same boat as many of the beetles and other creatures which ants welcome in their nests, obtaining board, lodging, and tolerance in return for services rendered (Chapter VIII). Their interest in the present connection comes from the fact that, though in normal conditions they keep their own young quite apart in chambers built by themselves, they can be induced, by being kept in artificial nests without any earth, to allow the Myrmicas to mix the broods of the two species. It is also interesting, as an example of ant plasticity, to find that, if they are kept by themselves in an artificial nest, they will after a time take to eating honey, insects, and other usual articles of diet, in spite of the fact that normally they take nothing but the product of the Myrmicas' social stomachs.

True slave-making has been evolved separately in the Formicine and Myrmicine ants. It was first observed by the younger Huber over a century ago, in the red slave-maker *Formica sanguinea*. The full biological meaning of its habit of raiding the nests of its black congener, *F. fusca*, for slaves, however, was not appreciated till nearly a hundred years later, when Wheeler found the clue to it in the habits of the queen. She is less independent than most other ant-queens, in that she is unable to found a colony by herself. After a successfully consummated marriage-flight she may either make her way into an established nest of her own species, or else into one of *F. fusca*. In the latter event, she collects a pile of pupæ, and kills any of the workers that attempt to take their possessions back. By the time the adult *fusca* workers hatch out, the robber queen must have acquired the proper smell, for they are wholly friendly, feed her, and tend the larvæ which hatch from the eggs she lays.

When adult *sanguinea* later emerge from the queen's own eggs, a mixed colony results. In different geographical sub-species of *F. sanguinea* different grades of slave-making propensity exist. In one the workers have none of it, and the mixed colony turns into a pure *sanguinea* with the death of the black workers kidnapped by the queen. In most, however, the *sanguinea* workers make periodic forays on nests of pure *fusca*, bringing back stores of worker larvæ and pupæ. This habit is given up by some races when the colony has reached a certain size; but, finally, in still others is permanently continued. The black workers in the mixed nests are not slaves in the ordinary human sense, since they do not perform more menial functions or in any way occupy a lower position in the social scale than the red workers; they are rather like captives given complete equality with their captors, but forced to change their nationality.

The fact that some queens, like her of *Formica sanguinea*, are unable to store in their bodies enough food to feed their first batch of young is the first step towards slave-making. In one remarkable case—Bothriomyrmex, temporarily parasitic on Tapinoma—the foreign queen approaches the host nest, and is then forcibly seized by the workers. Once in the nest, the workers often attack her, but she then leaps up on to the back of one of the pupæ or, often, of the host queen, who is a good deal larger than she. Apparently, in those positions her foreign smell is masked by the local odour of patriotism, for she is then perfectly safe, just as on another plane of behaviour a spy may be safe in a foreign country if he masks his real feelings by assumed devotion to the local institutions. She spends more and more time on the back of the host queen, slowly but surely accomplishing her task of sawing her head off. By the time this is achieved she has herself acquired the nest-smell, and is adopted, with the usual result that the Tapinoma workers rear up a brood of aliens, and the colony is eventually converted from pure Tapinoma to pure Bothriomyrmex.

Polyergus is allied to Formica; it also enslaves *Formica fusca*, but begins where the red slave-maker leaves off. The young queen here invariably invades some small colony of *fusca*, kills the queen by piercing her head with her mandibles—

definitely adapted to such pugnacious acts by their pointed strength—and is then adopted by the workers. The Polyergus workers are equally brutal in their raiding methods. The raids—always, for some mysterious reason, executed after midday—are highly organized, and any resistance on the part of the workers in the *fusca* nest merely results in the Amazons—as Huber christened the Polyergus—killing them with one nip of their sabre-jaws. Usually the *fusca* adults, whether as the result of instinct or experience, turn tail and leave their brood to the mercies of the hostile army. There is, in this case, a much greater division of labour between the captives and their captors, and the former more nearly merit the name of slaves. Polyergus' jaws are of purely warlike function, of no use in digging or capturing prey. They are a military aristocracy and do nothing but go raiding, while the *fusca* stay behind and do all the work of making the nest, obtaining food, and tending their captors' young. The masters have gone so far on the way to parasitism that they cannot feed themselves. Huber shut up thirty of them with some of their own young and plenty of food, but no slaves. Some actually died of hunger, and none even attempted to eat. A solitary slave was then put in. She at once fed the others, tended the larvæ, and began building operations. Another observer put a pile of sugar near a nest. Soon a number of slaves were gorging away at it. Some of the Polyergus then came out and pulled at the legs of the slaves. This was apparently a reminder of their duty, for they at once began to regurgitate to their masters.

When the colony migrates, it is the slave-workers which carry their captors to the new nest, while in the *F. sanguinea* the slaves are transported by the masters.

Finally come the ants which have reached the last stage of parasitism, and with it have lost the power of producing workers. The best known is Anergates, parasitic on Tetramorium ; but the step has been taken independently four or five times. The queen of Anergates, as in all these permanent parasites, secures her adoption by the host-workers by some unknown means; and then becomes swollen with eggs. The workers later, for reasons again unknown, murder their own queen. They tend the offspring of the usurper, all of which turn either into queens or males. The males afford a good example of what is known as neoteny, or reproduction while the body as a whole is still in an immature condition, since the general characters of the pupa-stage, including winglessness, are carried over into the adult phase. Mating must then take place within the nest, and is always between brother and sister; after mating, the winged queens fly out to seek new Tetramorium thrones.

It is interesting that most of the parasitic species of ants, and all those workerless permanent parasites, are scarce and very local; it is also interesting that the host is in every case closely related to the exploiter—this latter fact being explicable through the necessity for the workers to have nursing instincts adapted to the needs of the parasites' larvæ and pupæ.

CHAPTER VIII

GUESTS AND PARASITES

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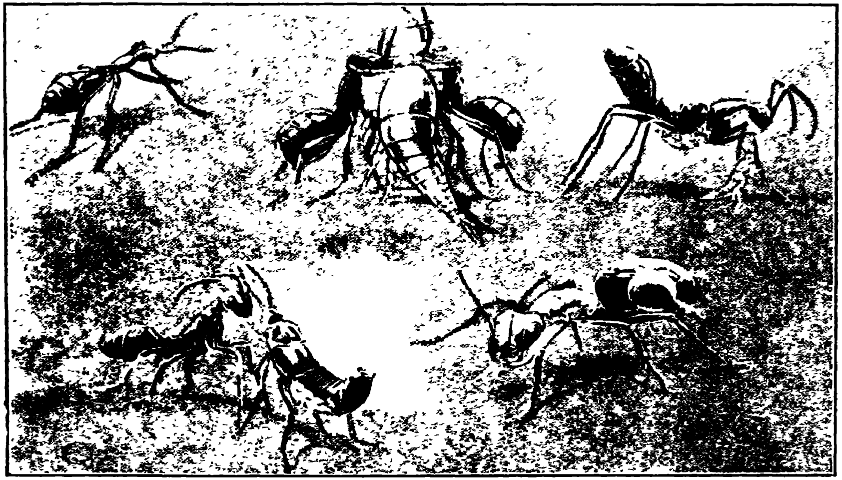
In one strange respect the social insects, notably the ants and the termites, have attained a specialization not reached by man; and that is in the number of animals of other sorts which live in their communities, and are so closely adapted to such life that they can exist nowhere else. It is, of course, true that in or about the habitation of man there are to be found plenty of animals of other kinds—physical parasites like flea and bug; economic parasites like rat, mouse, and cockroach; commensals like the cricket on the hearth or the house-martin; animals domesticated for food or draught, like hens, pigs, or horses; domestic companions and guards like the watch-dog; and pets like lap-dogs or parrots or goldfish. But the state of affairs is very different in the ants' nest. Their domesticated aphids and scale-insects we have already considered. There are no other kinds of domesticated animals, and no ant-pets deliberately taken into captivity because of their attractiveness. The same difference between insect and man, which has so often cropped up, is here again at work. Most of these "ant-guests" have been adapted to their mode of existence by natural selection, and their whole structure and instincts have been hereditarily modified. As we shall see, the tastes and aversions of the ants have doubtless contributed to the moulding of the guests' germ-plasm, but this moulding has been indirect, and there exists among the ants nothing similar to our conscious artificial selection, when we purposely breed only from those specimens of our pets or domestic animals which best please us, nor to an organized campaign against parasites or pests, like the ridding of Scotland of wolves or the Panama Canal zone from mosquitoes.

Finally, most of the aliens are of a size comparable to the ants themselves. If we imagined that in England our houses were, against our wills, inhabited by cockroaches as big as wolves and house-flies like hens; and that there were crickets to whose presence we were indifferent, although they were the size of our own children; and also pet-like creatures whom we liked because they rendered us some agreeable service, as it might be parrots which had the instinct of scratching our backs for us; or giant cats which we allowed

Plate VII



From "The Science of Life" by H. G. Wells, J. S. Huxley and G. P. Wells. (*Waverley Book Co., Ltd.*)

ANT GUESTS AND ANT ROBBERS. (1) A beetle, Mimeciton, which closely mimics the Driver-ants with which it lives. (2) The beetle Atemeles soliciting a worker Myrmica to regurgitate food for it by caressing the ant with its fore-legs. In return it will allow the ant to suck the secretion from the tufts of yellow hairs on its abdomen. (3) The silver-fish Atelura rushing up to snatch the drop of liquid food that one Lasius worker is regurgitating. (4) Another Lasius worker which is carrying three mites, Antennophorus, one under its head and one on either side of its abdomen. (5) A Honey-pot worker with two little beetles (Oxysoma) attending to its toilet.

to eat our babies in their cots because they secreted hot rum-punch or some equally fascinating liquid; and that in France, say, and the United States there were similar sets of animals, willy-nilly sharing men's houses and reproducing there, only all belonging to different species from those in England; and, finally, that they were all incapable of existing permanently anywhere outside our houses; then we should begin to get some idea of the menagerie of guest-animals in the habitations of ants.

The evolutionary method which a great many of these creatures (and probably that further group to which the ants show active friendliness) have adopted is to exploit their hosts' peculiar form of greed, which, in turn, has been specialized as a consequence of their trophallaxis. They have developed glands producing secretions similar to those exuded by the ant-larvæ themselves, and in return for the privilege of licking up these tasty juices the workers will feed them just as they feed the larvæ. Sometimes the secretions of the guests must be possessed of new and overpoweringly attractive properties to the taste, so that the nurses even neglect their proper charges in favour of these aliens. We know, alas! of human parents who will neglect their children for drink, but this is as if a mother were to abandon her baby for the charms of gin exuded from the body of a changeling.

Wheeler admirably sums up the situation as follows: "Any insect possessed of these glandular attractions . . . can induce the ants to adopt, feed, and care for it, and thus become a member of the colony, just as an attractive and well-behaved foreigner can secure naturalization and nourishment in any human community. But the procedure among the ants is more striking because the foreigners are so very foreign. . . . Were we to behave in an analogous manner we should live in a truly Alice-in-Wonderland society. We should delight in keeping Porcupines, Alligators, Lobsters, etc., in our homes, insist on their sitting down to table with us, and (in some cases) feed them so solicitously that our children would either perish of neglect or grow up as hopeless rachitics."

Perhaps the strangest of these alien exploiters are the Staphylinid beetles, Lomechusa and its relatives. The habits of Lomechusa were brought to light by the Jesuit entomologist Wasmann. It lives exclusively in the colonies of the red slave-maker, *Formica sanguinea*. The adult beetle solicits food from the ant-workers by stroking them with its antennæ; its abdomen is covered with bunches of golden hairs, called trichomes, which surround the opening of special glands and act in lieu of teats for their secretions; the beetles present them to the ants, working their abdomen forward over their back; and the ants eagerly suck off the oily secretion, rewarding the beetles with regurgitated food. The grub-like larvæ apparently exude fatty secretions of much price, for not only are they fed with regurgitated food by the worker-ants, not only are they tended and moved about with the ants' own brood, but are allowed to eat the ant-larvæ. Indeed, the ants appear to prefer the Lomechusa grubs to their own, with the result that a large part of the brood dies.

It is in colonies heavily infected with Lomechusa that pseudogynes (p. 34) are produced. It has been supposed that the ants eventually realize the shortage of workers and attempt to convert queen larvæ into workers by altering their diet—but too late to have effect. Another possible explanation is that the queen larvæ, being neglected, fail to get the right food and are therefore switched over towards the worker type of development. These pseudogynes, which usually comprise five per cent. and may reach twenty per cent. of the population of an infected nest, are described as "lazy, cowardly, and incompetent." When a nest is heavily infected it can produce no queens, and will soon die out.

It might be thought that the whole race of red slave-makers would be on the road to rapid extinction owing to the beetles. But, as a matter of fact, the species is abundant and prolific, the parasites' infection only local and sporadic; and this is true, not only of this host and this parasite, but of all other deleterious ant parasites and their hosts, whether the parasites be insects of other groups or ants of slave-making or parasitic habits. The greatest danger to a deleterious parasite is to be too effective in inflicting harm upon its host. For if the host decays, it decays too ; if the host is extinguished, it, too, becomes extinct. In general, it is the very widespread successful or plastic species that support the greatest number of kinds of parasites, because they are less likely to succumb under the burden. The extraordinary abundance of gall-producing insects that affect the oak is an example from another group. In addition, if the parasite is not to kill itself by killing its host, its numbers must be kept down, either by the host's acquiring partial immunity, or by great difficulties of dispersal from host to host, or by some other means. Thus, as a general law of parasite existence, the parasite must be less numerous or in some other way less biologically dominant than its host.

The check on Lomechusa is a very curious one. The ants treat the beetle-grubs as they do their own brood. This ant buries its full-fed larvæ in the soil; here they spin cocoons, and are then, as pupæ, dug up again, cleaned, and piled in special chambers. Now, the Lomechusa larvæ, though they, too, must be buried to pupate, spin no cocoons, and infallibly die if dug up again; so only those few buried beetle-pupæ which the ants fail to unearth succeed in turning into adults, and the population of Lomechusa is thus regulated down to sufficiently low proportions.

The closely-related beetles Atemeles and Xenodusa are interesting in that they have two hosts: in the summer they live in Formica nests, but take up their winter quarters with species of Camponotus, the carpenter ant. They only breed, however, in the summer, so that the Camponotus does not have its brood affected, and produces no pseudogynes.

Several hundred species of befriended guest-beetles are known from ants' nests. All of them possess the special glands and their teat-like trichomes. Curiously enough, the hairs of the trichomes are almost always yellow, and the general colour of the beetles an oily red. In addition, their jaws are often highly specialized to feed on the liquid pumped up by the ants, and their antennæ modified to imitate the soliciting action of the antennæ of other ants. The addiction of the ants to the liquors and rich buttery sweetmeats which these produce is revealed in the way in which, at the threat of danger, they seize the beetles and carry them to safety.

Other kinds of insects also exploit the ants' greed. During the last decade, for instance, it has been discovered that, of all unlikely creatures, some of the lovely blue butterflies (*Lycænidæ*) are, at one stage of their development, ant-devourers. The caterpillar lives the usual vegetarian caterpillar life until it is half grown. It then descends from its food-plant and stations itself in an ant-track. It appears to produce desirable secretions, for the ants, on finding it, carry it off to the nest, where it lives at the expense of the community, giving only luxuries in return for necessities, until the time comes for it to pupate.

Other ant-guests, not being ambulatory bars or confectioners' shops, are treated with hostility by the ants, and must gain their living by stealing and escape destruction by agility or strong defence. For instance, *Lepismina*, a primitive wingless insect of the silver-fish type, steals impudently from Lasius. Janet has described the scene when the worker Lasius bring back food to the nest. The *Lepisminas* at once begin to show by their excited movements that they smell something. The returning workers meanwhile begin to regurgitate food to their stay-at-home sisters. As the food is being transferred, feeder and fed face each other, with the fore-parts of the body raised. A thief approaches such a couple, crawls below their heads, suddenly snaps up at the liquid as it passes from mouth to mouth, and rushes off. The ants, being in rather a delicate pose, are usually not able to turn in pursuit before the *Lepismina* is out of reach; and, in any case, it is covered all over with smooth scales, which render it hard to catch.

Another thief-guest relies on mechanical protection. It is compassed all round with a series of long scales, somewhat in the shape of the long caparisons worn by mediæval horses in the tourney; some of these scales can also be thrown forwards to form a more or less tubular protection for the proboscis. In addition, there are stiff bristles which protrude straight out from its flanks. It, too, steals from the workers as one is feeding another, reaching up with its protected mouth. If an ant tries to get under its defences, the bristles act like cats' whiskers to give notice of the attack, and the scales on that side come down flat on to the ground, conferring upon the attacked side of the animal the properties of a tank.

Then there are parasites—thieves, if you will—of which the ants take no notice. Wheeler has described the larva of a little fly (*Metopina*) which exploits an ant of the genus Pachycondyla. The fly-grub clings like a collar round the neck of the ant-grub; the latter is fed by having pieces of insects placed in a natural trough on its ventral side; and on this happening the Metopina uncoils and reaches out for a share. Apparently it acquires the smell of its host, for the ants do not notice it at all, and clean it with the rest of the ant-grub. Its adaptation to safe emergence deserves mention. Its development is adjusted to that of its host-grub, and when the ant-larva pupates, the fly-larva, which is, of course, enclosed in its host's cocoon, moves to the hind end and there pupates also, forming a puparium very much flattened against the cocoon wall. When the callow adult ant is ready to emerge, the workers bite open the front end of the cocoon and pull it carefully out, and the apparently empty cocoon is then taken off and thrown on the refuse-dump. The fly's pupal period has been adapted by natural selection to be longer than the ant's; thus when the fly emerges, it finds no obstacle to a safe exit. Here, again, the parasite merely takes toll from the ants' excess; there is no sign of its inflicting any damage on the individual larva from which it steals or on the colony as a whole.

The most extraordinary of tolerated guests is perhaps the externally parasitic mite Antennophorus, some of which infest those same Lasius which we recorded as being almost blind and keeping white ant-cows underground. The mites are quite large in comparison with their hosts, much like a cat or a smallish monkey in relation to a man, yet up to four (or rarely six) may be found on one ant. They behave in a remarkable way as regards the positions they take up, always placing themselves so that the ant's balance is not upset. When there is one, it is always under the chin; if a second comes, the two move to the two sides of the abdomen; a third will occupy the place under the head; a fourth will occupy one side of the head, while the third will move to the other; a fifth will once more attach itself below the chin; and the rare sixth will occupy the only vacant space, on the top of the abdomen.

The ones attached to the head feed on regurgitated drops as they pass directly between the mouths of their own St. Christopher and another ant; or they cause it to "cough up" for their sole benefit by stroking it with their fore-legs, which are moulded into a passable semblance of ants' antennæ. Those mites which ride on their host's abdomen stroke other ants, or snatch at drops passing between other worker-pairs.

The strange fact is that the mites appear not to produce any secretion in exchange; and the ants try to throw off their riders when they are mounting, though afterwards they tolerate them once they have settled into their positions of equilibrium. One can only conjecture that the mites have the nest-smell, that once in position they are not much of an annoyance, and that their soft strokings are like enough to the solicitations of other workers to delude their hosts. Wheeler suggests that the blind ants feel towards them as we might to pleasant pets; this may, of course, be so, but seems on general grounds rather unlikely.

These instances constitute but a sample. Already more than 2,000 separate species of ant-guests are known, somewhere about half the number of known species of ants; and these include representatives of mites, spiders, crustacea, and most of the orders of insects—indeed an amazing menagerie! "Where the feast is, there shall the vultures be gathered together"; and the very success of ants has led to their being exploited by these hordes of other creatures.

CHAPTER IX

TERMITES OR "WHITE ANTS"

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WE cannot exclude termites from our survey. For though actually quite unrelated to true ants, they are so like them in many ways as to have earned the name of "White Ants." The organization of their colonies is very like that of ants' nests, and yet sufficiently different to afford much food for reflection. In many ways they excel even the ants in strangeness of habits and social organization; but for all their abundance and their marvels of structure and instincts they have not attained the same supremacy in the biological world. They still bear the marks of their origin from an altogether lowlier stock of insects; hardly any of them can tolerate daylight, and they have not been very successful in pushing far out of the tropics.

They belong to the Isoptera, one of those primitive insect orders which have no true metamorphosis, but hatch from the egg in a form essentially like the adult. Almost all of them are tropical or sub-tropical. A few penetrate to higher latitudes; but in striking contrast to the ants, there are not more than forty species or so in the United States, and only two of them reach the parallel of Boston. Not only this, but whereas the highest sub-families of ants are the most successful in invading cool climates, the highest family of Termites, the Metatermitidæ, is almost exclusively tropical.

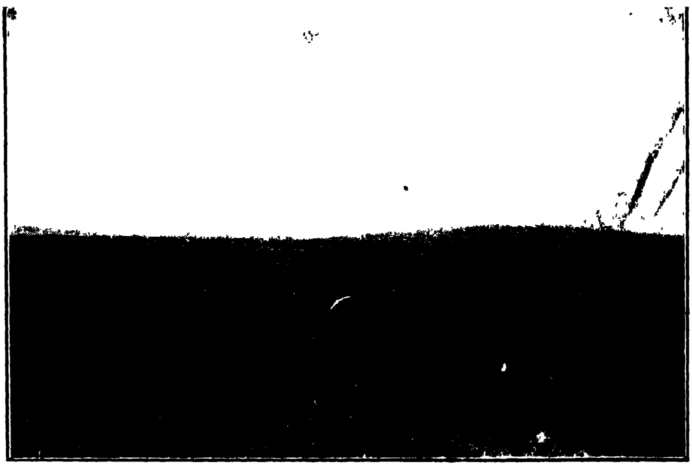
They may be divided very conveniently into four families, arranged in a single scale of progressive specialization. One of these, the Mastotermitidæ, comprises but one living species confined to Australia, though fossils show that in the early tertiary epoch the family was widely spread in Europe, and probably elsewhere. Thus Mastotermes has the same sort of relation to higher Termites, both in structure and distribution, that the duckbill Platypus has to the remainder of living mammals; and just as the Platypus betrays the relationship of mammals to certain reptiles, so Mastotermes shows that Termites are sprung from Orthopteran ancestors, since it betrays close affinities to a family of cockroaches, the Protoblattidæ, which died out in the Permian period.

All Termites are fully social, with neuters doing the work of the colony. But there are two, and probably three, fundamental distinctions between their social organization and that of ants, bees, and wasps. In the first place, the colony is always started by a "royal pair," a queen together with the male who has fecundated her, instead of by a solitary queen. Secondly, the workers, and other neuter castes when present, are of both sexes in equal numbers, instead of all being sexually-arrested females. And, thirdly, it is probable that the various main castes at least are all determined by heredity, and not by means of differences in diet. Thus the sexes are of equal social importance instead of the males having a purely reproductive function; and, if the third point be established, the social organization is in a sense on a lower level than that of ants or bees, since the determination of the various castes depends wholly on a germinal mechanism, and not at all on the instincts of the nurses.

There exists a complete gradation from colonies with only a few score individuals, and only one type of neuter caste, up to communities which pass the million mark, outdoing even the ants in numbers, and exhibit an extraordinary polymorphism. In the most developed communities there exist the following types: (A) *Reproductive caste.*—(1) First-form reproductives ("queens" and "kings"); (2) second-form reproductives, or substitute queens and kings; (3) third-form reproductives, or worker-like substitute queens and kings. (B) *Worker caste.*—(4) Workers, male and female. (C) *Defence caste.*—Either (5*a*) soldiers or else (5*b*) peculiar snouted defence forms called the *nasuti* or "nosy ones," these also both male and female. This makes ten castes, five male and five female. In addition, both the workers and the soldiers may be differentiated into sub-castes, differing just as in ants in size and proportions of heads and body, bringing the total numbers of distinguishable forms up to twelve or fourteen.

In almost all Termites the young reproductives alone among the castes are fully pigmented and capable of facing the light of day. They are winged, but, like the queen ant, break off their wings on descending to earth, after leaving the nest on their one flight. This flight is not a true nuptial flight, but a dispersal flight, since mating takes place, not in the air, but after they have descended (in couples) to the ground, and shed their wings. Later, the queens grow to an incredible size, flabby white sausages over four inches long, and proceed to lay an egg about every two

(*a*) A Termite Queen (p. 120). The head and thorax are to the left. The abdomen has been stretched by the expanding ovaries until the skin is translucent. This queen laid over 2,000 eggs during the night after being dug out of a nest in Kenya.



Photos by J. S. Huxley

(*b*) The abundance of termites in the tropics; many hundreds of termite nests on a plain in Western Uganda.

or three seconds for the remainder of their natural life, which may last for years.

The second-form reproductives have all the characteristic organs of the reproductives, but reduced in size or quantity—less pigment, smaller brain, eyes and reproductive organs, and rudimentary wings; while the third-form reproductives carry the loss a step further, and have no wings, scarcely a trace of pigment, rudimentary eyes and further reduced brain and gonads. These two castes, of substitute queens and kings, are what we have called neotenic (p. 97); they carry over the more primitive characters of the later or earlier larval stages into the adult reproductive phase; their origin would be accounted for on the hypothesis that all processes of differentiation, save the one concerned with ripening the gametes, were slowed down during their development. Their function in the colony is somewhat obscure. They are usually believed to be reserve reproductive units, ready to take the place of the true kings or queens should they die; but this is not certain, nor whether they, as well as the full kings and queens, normally exercise their mating instincts. In the colonies of some species the true queen never develops, but her place is taken by a harem of second-form females, sometimes over a hundred in number.

The workers are white and pigmentless, lack wings, and their eyes are rudimentary or absent; like the independently evolved worker-caste of ants, they are chiefly concerned with nest-building, food-seeking and food-distribution, and the toilet of the other castes; but unlike worker-ants, they have brains smaller than the reproductives. The soldiers are wingless, with huge heads and jaws, and usually use them in the defence of the colony. They have some hardened and pigmented skin, but only on the head; and thus they are like the goblins in McDonald's "Curdie and the Goblins," cast-iron in the head but soft and defenceless elsewhere. Since they, too, are permanently subterranean, their eyes are degenerate. The *nasuti* also defend the colony, but in a way which has the same sort of relation to the brute strength method of the soldiers as has chemical warfare to bayonet fighting. Their jaws are minute, but in return the frontal gland which most termites possess is in them much enlarged, placed conveniently forward at the tip of the snout, and made to secrete an adhesive liquid which certainly can immobilize the enemies by sticking their limbs and antennæ together, and perhaps has poisonous properties as well.

In some forms the secretion of the *nasuti* appears to be used to dissolve hard substances which are in the way of the workers when building; it is stated that even concrete may be eroded in this way!

Miss Thompson has discovered that the young reproductive forms can be distinguished from the worker or soldier at hatching, and probably the worker from the soldier also, by differences in the size of brain and eyes. This would make it practically certain that at least the three main castes were predetermined at the moment of fertilization, just as are the sexes in most animals, or the different forms of flowers in primrose or loosestrife. The sub-castes or workers and soldiers, however, are presumably determined, as in ants, by differences in the amount of food secured by the growing young combined with differential powers of growth in different parts of the body. The origin of the subsidiary royal forms is unknown.

How the genetic machinery works we have at present not an inkling. It has been further asserted that while the first-form royalties can reproduce all the castes, the second-form reproductives cannot give rise to the first form, and the third form neither to the first nor to the second form. The mechanism underlying this is equally obscure, though it, too, might be genetic in nature, the two substitute forms being recessive.

The food economics of the termitary outdo those of the ants in strangeness. To start with, the higher, wood-eating termites are unable to digest their food unaided; they have to rely on certain parasites turned helpers. These symbiotic inhabitants of their gut are ciliates called Trichonymphids, large for single-celled animals, with bizarre movements and a very peculiar arrangement of their cilia. They are normally only found in the interiors of the adult workers and soldiers, not in the young, nor in the reproductives.

Now, in higher termites, the whole termitary derives its existence almost entirely from wood, and other dead plant tissues which consist either of cellulose or the modified woody cellulose, lignin. Neither cellulose nor lignin, however, are attacked by the digestive juice of any animal higher than snails. The Trychonymphids, on the other hand, produce cellulose-splitting ferments; they thus supply their hosts' deficiencies. The termites supply the food for both partners; the protozoa chemically chop it up until it is soluble, and both live on the products of their joint activity. The reason why Trichonymphids only live in the workers and soldiers is doubtless that these alone eat raw cellulose, the other castes being supplied by them with liquid products of digestion.

Experiment has proved what observation suggested—the indispensability of the Trychonymphid for the termite. The protozoa cannot stand much pure oxygen; in an oxygen atmosphere all of them die in a few days, while the termites themselves are quite unaffected. Workers thus rendered protozoa-less die of starvation in a few weeks, although provided with all the wood their hearts could desire. They devour the wood with all their ordinary appetite, but nothing happens to it in their interiors, and it passes out unchanged, without their profiting from it in the slightest. If, however, they are artificially reinfected, they become capable of digesting their food once more.

The food, once digested in this way, begins a direct or indirect circulation through the colony, compared to which the ants' methods are primitive. This food circulation has been likened to the circulation of blood and lymph through our own bodies; and, though the comparison is but rough, yet it is exact in one fundamental respect—the food does constitute a nutritive stream, by which the various units of the whole are bound together in mutual dependence. First, as in ants, the termite workers regurgitate, but what they regurgitate is only partially digested. Secondly, they can dispense more fully digested food, but this must be done *per anum*, only part being absorbed in its passage through the intestine, and the rest passed out behind for others' consumption. Thirdly, some of the absorbed food is worked up in the "salivary" glands into a liquid with nutritive and doubtless pleasing properties, and drops of this are secreted for others. It seems probable that the different castes exude different substances, and that, in the darkness of the nest, they are recognized by their taste. The full-grown first-form queen appears to secrete the most delicious exudate of all, and is invariably seen to be surrounded by a regular court of workers, who, however, are not doing obeisance, nor even tending her, but licking up the royal juice as it exudes, sometimes with such gusto that they perforate the royal skin.

Just as in ants, this fondness of the termites for such rich food has led to their exploitation by a number of guest-insects who have mastered the secret of producing similar substances. Presumably in accordance with differences in the construction of termites' mouths from those of ants', their guests have not developed the teats of hairs characteristic of ant-guests, but instead have produced thin-walled, lickable structures, swollen bellies or special protrusions of the body. In addition, a great many have acquired the physogastry or extreme swelled-belliness characteristic of the full-blown termite queen. This is usually produced by the enlargement of the fat-body, but may be due to enlarged gut or gonads. With increase of abdomen, there generally goes decrease of head and eyes, thorax and wings. A curious fact about the guest-beetle Spirachtha is that it appears to hatch out in more or less beetle-guise, and only (like the termite queen) to acquire the swollen belly and lickable outgrowths later.

It would naturally be supposed that this swelling was directly concerned with the production of more fatty delicacy, and more surface off which it could be licked. However, it appears to be the fact that some of the insects which are never licked, but to which the termites are either indifferent or hostile, also acquire physogastry. It has been accordingly suggested that physogastry is in part due to some substance in the food acting like a hormone, and that selection has later stepped in to exaggerate and utilize the result.

There are no examples known of slave-making or workerless parasitic termites species; in fact, the social insects most frequently nesting inside or near termitaries, and profiting by the shelter, protection, and food provided, are ants. A few termite species, however, are thieves, and some *Microtermes* steal fungus and prepared "soil" from the vegetable-gardening termites *Odontotermes* and with the spoils make gardens of their own.

The nests of termites are on the whole more interesting than those of ants. This is natural, since the termite is so intolerant of light and air that, unless it lives wholly under the level of the soil, it requires something more solid and permanent. If, as from one point of view we are justified in doing, we regard the termite colony as one individual, then the nests of higher termites are to be compared with the thick armour-plate of giant crabs or tortoises or some dinosaurs, or the shelly fortress of an oyster or a conch. But armour-plate, however successful an expedient for the time, in the evolutionary long run leads animals into a blind alley. The more efficient the dinosaur's armour, the less need of speed, brain, or acuteness of sense to avoid enemies; the more colossal and steely-sided the termitary, the less readily can its inhabitants change their abode, the less are they forced into a healthy give-and-take with the forces of Nature. Thus in the long run the termites have become a race of gnomes, stranger and more remote from the main stream of life than ants or bees, supreme within their own limited darkness, but in a sense aliens in the greater world.

The lower termites in general make nests not unlike those of ants, diffuse tunnellings below ground, or in decaying logs and stumps. The higher types, on the other hand, build what have been styled concentrated nests, definite edifices sharply marked off from the rest of the environment. Perhaps the most striking are the giant earthen termitaries of the African grasslands, which, gradually built up over the original tiny subterranean chambers excavated by the royal founders, may reach a height of twenty feet and more, so strong in construction as to be almost indestructible with anything less powerful than dynamite. Very similar nests are to be found in Australia, too. In the hottest part of this latter continent some species construct long, thin, wedge-shaped buildings, which are called compass-nests owing to their always being aligned north and south; this arrangement doubtless is an adaptation to the great heat, since less surface is thus exposed to the midday sun. In Africa, strange stalked nests are found, with a mushroom top apparently serving as an *en tout cas* to protect both against sun and rain. Other nests from the rain-forests of the same continent bulge out like a cluster of sausages from the trunks of trees, and are protected from the rain by a whole series of inverted V's of cemented wood-pulp built on to the tree-trunk above them. While the ground-nests are usually built of earth, the material of the tree-nests is for the most part chewed and semi-digested wood cemented with saliva into a paper-like mass. Usually they are round or oval, and may reach the size of a respectable barrel. Termitaries, unlike ants' nests, never have any visible entrances. This is owing to the light-shunning of their inhabitants. The termites either burrow through the surrounding soil or wood, or, in many of the higher forms, though they travel on the surface of the soil, run up tunnels over their roadway as they advance.

These tunnels may be several score yards long, and by their aid the colonial organism extends its tentacles in every direction. When a large termite colony by this means penetrates into a house, its ravages may for a long time remain unsuspected, since the workers will devote themselves to eating out the inside of every wooden object available. Eventually, they will reduce walls, floor-planks, tables, and chairs to a mere shell, and the householder is made aware of what has been going on by the collapse of his furniture or his house.

Owing to these habits, termites are much more destructive than ants. It is, of course, not only the woodwork of houses which they invisibly devour. Fences, railway-sleepers, telegraph poles, boats, landing-stages, bridges—all are grist to their mill. But it is not merely material civilization whose spread they retard. Paper, too, is made mainly of cellulose, and the addition of printer's ink unfortunately does not render it unpalatable to the termites. Thus some of their most serious ravages are committed on documents and books. Von Humboldt records that, when he was in the hotter part of South America he rarely saw any book over fifty years old, the rest having gone to feed termites. It has been suggested with a good deal of reason that this is one (though doubtless by no means the only) cause of the slow development of culture in the tropics; and it is certain that any tropical nation that wants a flourishing and enduring civilization will have to construct, what some have already made a beginning with, termite-proof foundations for its buildings, more particularly the buildings where its libraries and its archives are housed, and for any structure in which any degree of permanency is required.

On the credit side of the termites' account, however, must be entered the fact that, unlike ants, they are not only not deleterious but actually beneficial to agriculture. In temperate regions, as Darwin showed us, earthworms perform a very important task in preparing and renewing the soil for plants. Termites perform a very similar function in the tropics, but probably on a greater scale, and certainly with greater rapidity. Their tunnellings aid mechanically, their protozoan digestion chemically, in hastening the disintegration of those resistant substances, cellulose and wood; and in this way much of the capital of life, which would otherwise stay locked up for years in a strong-box of chemical unavailability, is by them rapidly brought back into circulation.

Strange to say, fungus-gardening has arisen in termites as well as in ants—a good example of independent evolution which may be taken to heart by some of the more radical diffusionists who maintain that in human culture nothing has ever originated more than once. The fungus-gardens may reach an even greater size and perfection than in the ants; the nests containing them are sometimes provided with chimney-like structures, which are probably ventilating shafts designed to help in the regulation of temperature and moisture. It has at any rate been shown that the diurnal range of temperature in the nest is only 9° C., when that outside is over 20° C. The workers and soldiers keep to the more solid diet of cellulose, and leave the fungus to the reproductives and the young. The young use the gardens as a combination of pasture and nursery, and present a pretty enough picture as they browse —white miniature lambs against herbage of equal whiteness.

It can be prophesied of the termites in their armoured colonies, with even greater assurance than of the ants, that they have reached the end of their evolutionary tether, and will continue, as a group, with no essential change and no real progress. Holmgren, one of the authorities of the group, has pointed out that their évolution is accompanied first by that specialization of their societies which has already been mentioned, secondly by an enlargement of their brains, and thirdly by a degeneration of their bodies. This is a fate which has often been prophesied for the human species. It remains to be seen whether the fact that man lives partly on the level of reason and foresight will enable him, through sport, physical exercise, and eugenics, to surmount the danger.

CHAPTER X

ANTS AND MEN

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So our brief review of the ants and termites comes to an end. We are now in a better position to judge of the fallacies into which so many writers on social insects have fallen, to some of which reference has been made in the introduction to this book.

A few have been guilty of gross over-simplification. Bethe, for example, wished to make of ants and bees the merest reflex machines, incapable of profiting by experience or recognizing the locality of their nests in any way at all similar to our recognition of familiar spots. Others, again, would have it that they were wholly colour-blind, which, if true, would have robbed the brilliant colouring of flowers of all biological meaning.

But the majority adopt a more popular and a more insidious view. They either turn insects into miniature human beings, or else ascribe to them wholly magical attributes. Bethe himself was obliged to postulate in bees a mysterious sense of direction which operated through none of the ordinary channels of sense; and the powers ascribed to instinct by writers such as Fabre would enter the realm of miracle—if they were true. On the other hand, lay writers, like Maeterlinck in his book on *The Life of the Bee*, and still more that on *The White Ant*, ascribe all the achievements of insects to intelligence, and draw invidious comparisons between their minds and that of man. It would really seem that such writers have never heard of Darwin, or at least never read his works or even a modern summary of what is meant by Natural Selection; that they are ignorant of ordinary physiology, and unaware of the extreme complexity which wholly mechanical and non-conscious behaviour can reach in ourselves.

Maeterlinck, for instance, says that the termites are more intelligent than we are because they have found out how to digest wood and dissolve concrete, and can mould the bodily form of their citizens at will, sterilizing them, turning them into born soldiers, or making them mere egg-laying machinery. But the termites can no more help having the wood-digesting protozoa in their gut than dogs can help having worms, and, since no one has ever thought of ascribing to human intelligence the existence of the admirable ferment trypsin in our pancreatic juice, or the fact that our eyes are constructed as very efficient cameras, there is not the slightest reason for doing so in the case of the termites' chemical achievements. In termites, too, there is every reason to suppose that all the castes are predetermined by heredity; if this were so, their "intelligence" in possessing royals, soldiers, and workers would be precisely on a par with the "intelligence" of human society in generating people who are fair-haired or dark-haired, tall or short, temperamentally athletic or intellectual.

Even where, as in ants and bees, the differences between neuter and queen are determined by feeding, the whole capacity for reacting to the two diets in these two different ways is given by heredity, as is also the instinct of the workers to feed the young in these particular ways—for they will do so without any training—and the only point left to be decided by "intelligence" is the relative numbers of queens and workers to be produced. As a matter of fact, we do not yet know anything as to how the right proportion of the castes is arrived at, and it may even be accomplished by some almost automatic response. In any case, the actual bodily shape of the different castes has been arrived at through the operation of natural selection, and is wholly different from the moulding of his domestic animals and plants achieved by man, as when the fancier breeds a new strain of fowls up to a standard previously laid down, or Sir Reginald Biffen deliberately sets about creating a new sort of wheat.

Finally, there is another fallacy which from time to time crops up. We are told that, as we elaborate our civilization, as we mechanize it by trusting to the achievements of applied science, as we specialize more and more in occupation, we are inevitably heading for a condition in which our society will come to resemble an enlarged ants' nest or gigantic termitary. For this prognostication, too, which has been recently advanced by Dean Inge, among others there is no shadow of biological support. Partly, it seems, this view is based upon conscious or unconscious Lamarckism; it is felt that, if we specialize, the structure and modes of thought of our offspring will gradually become fixed in the grooves of society's various specialisms. The modern study of heredity has luckily proved the baselessness of any such fear. For the rest, it is based on a particular theory as regards the course of evolution. All types or groups of animals and plants—say the upholders of this view—pass through a period of rapid evolutionary change to reach a later phase of stability. The first phase is characterized by great plasticity of the germ-plasm, while in the second it becomes fixed and resistant to change.

Now, in the first place, this idea of the plasticity or fixity of the germ-plasm is pure hypothesis, proposed as a possible explanation of the undoubted fact that many types, after rapid initial evolution, do settle down later to a slowing or stoppage of progress. But it by no means follows that the cause of this resides in the germ-plasm; it may just as well depend on the animal having become so specialized that few or no changes which actually take place in the germ-plasm could be of any biological advantage. And, in the second place, the fact that rapid rise, followed by stability and finally by decline, has frequently occurred during evolution is no reason for erecting a universal law upon the body of the facts, any more than the frequent rise, stable maturity, and eventual decline of nations is any valid reason for supposing that such a cycle is a necessity for all nations.

It is always possible, in the past instances of such evolutionary cycles, to assign reasons for the slowing down of progress and the eventual decay or extinction of the group. The limits of physical specialization account for the one, and the rise of new groups from an initial stage a step higher than that of the earlier group, a rise frequently aided by cosmic accidents such as changes in climate or in the distribution of land and water, accounts for the second. If one specialization can be achieved without enslaving the body and turning it into a particular kind of tool-box, and progress, too, can take place by the aid of conscious methods, by improvement of tradition and social organization, and if necessary by deliberately controlled breeding, the whole case is altered, and the limitations fall to the ground like the walls of Jericho at the blast of the Israelites' trumpets. Man alone among animals has fully passed from the one condition to the other. It is curious that a writer who, like Dean Inge, has so acutely criticized the idea of inevitable progress should not have applied the same criticism to the idea of inevitable arrest of progress.

Be that as it may, the ants and the termites are still on the biological level on which, though mind has come to play a considerable part in individual and social behaviour, the evolution of the race is still entirely dominated by blind and automatic forces such as natural selection. Man, on the other hand, is on the level where evolutionary change can be brought about by changes in tradition and by conscious purpose, applied either to this tradition or to the germ-plasm of the race.

There is thus no reason to suppose that man is destined to sterilize nurses or manual workers, to breed armoured or gas-resistant soldiers, communal parents the size of whales, or an intelligentsia all head and no body. Nor is there any reason to suppose that he will settle down into a mechanized and stable condition of existence—at any rate, for the long millions of years where there will still be things for him to discover, still new enjoyments to taste, and still new changes to make by which the life of society and of the individual may be improved. By virtue of his nature, he knows that he can discover new truth, can create new works of art, can control his own destiny; and this is precisely what even the most intelligent ant or the most specialized termite entirely, inevitably, and for ever lacks.

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